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Simulation Modelling Tools to Evaluate Alternative Fishery Closure Area Network Designs for Shallow-water Benthic Invertebrates in British Columbia

N.M.T. Duprey, J.M.R. Curtis, J.L. Finney, and C.M. Hand

Fisheries and Oceans Canada
Science Branch
3190 Hammond Bay Road
Nanaimo, BC V9T 6N7

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

The suitability of alternative tools or proxies for designing fisheries closure area networks depends first and foremost on the management objectives and how these are articulated in an operational sense. For instance map-based approaches (e.g. habitat suitability models, MARXAN analyses) may be appropriate in cases when management objectives are expressed simply in terms of a target area to be incorporated into the network. Alternatively, more sophisticated simulation models that account for dynamic interactions between fisheries, populations, and environmental processes (e.g. ocean circulation) may be required when management objectives are expressed in terms of changes in the patterns of distribution or abundance of species. In this paper we describe and apply a set of quantitative tools that can be used to provide advice on the number, size and spacing of fishery closure areas. The tools build on software packages and programs (ArcGIS, RAMAS, R, GRIP) that are currently available and being applied to address a broad range of marine spatial planning objectives. Together these tools form key components of a simulator that couples four sub-models of habitat suitability, metapopulation dynamics, dispersal and fisheries management. We apply these tools to demonstrate how they might be used to inform decisions on fishery closure area design in Area 12 using *Parastichopus californicus* as a case study species. We show how the results of a model sensitivity analysis can be used to evaluate alternative network designs using a range of performance criteria. We conclude with a discussion of how the set of tools may be applied to address a broad range of spatial management questions for a broad range of species in any area provided sufficient data are available.

Outils de modélisation pour simulation visant à évaluer différents réseaux de zones fermées à la pêche des invertébrés benthiques des eaux peu profondes en Colombie-Britannique

RÉSUMÉ

La pertinence des différents outils ou indicateurs pour la conception de réseaux de zones de fermeture des pêches dépend d'abord et avant tout des objectifs de gestion des pêches et de leur définition sur le plan opérationnel. Par exemple, les solutions cartographiques (p. ex., modèles de qualité de l'habitat, analyses MARXAN) pourraient s'avérer utiles dans les cas où les objectifs de gestion sont exprimés simplement en fonction d'une zone cible à intégrer au réseau. Par ailleurs, des modèles de simulation plus sophistiqués qui tiennent compte des interactions dynamiques entre les pêches, les populations et les processus environnementaux (p. ex., la circulation océanique) peuvent être nécessaires lorsque les objectifs de gestion sont exprimés en fonction des changements dans les tendances en matière de répartition et d'abondance des espèces. Dans le présent document, nous décrivons et utilisons un ensemble d'outils quantitatifs pouvant servir à fournir des avis sur le nombre et la taille des zones de fermeture des pêches ainsi que l'espacement entre celles-ci. Ces outils sont inspirés de progiciels et de programmes (ArcGIS, RAMAS, langage de programmation R, IGOT) actuellement disponibles et appliqués à un vaste éventail d'objectifs de planification spatiale marine. Ensemble, ces outils constituent les éléments clés d'un simulateur qui regroupe quatre sous-modèles : habitat propice, dynamique de métapopulation, dispersion et gestion des pêches. Nous appliquons ces outils pour montrer comment ils peuvent servir à éclairer les décisions sur la conception des zones de fermeture de la pêche dans la zone 12 au moyen de *Parastichopus californicus* comme espèce à l'étude. Nous démontrons comment les résultats d'une analyse de sensibilité du modèle peuvent servir à évaluer d'autres conceptions de réseaux au moyen d'une gamme de critères de rendement. Pour conclure, nous analysons la façon dont la trousse d'outils peut être appliquée à une large gamme de questions de gestion spatiale pour un large spectre d'espèces se trouvant dans une zone donnée, à condition de disposer de suffisamment de données.

1. INTRODUCTION

Marine reserves are being designed and implemented around the world because they help protect ecosystems and to facilitate the management of single or multi-species' of fisheries (Halpern 2003). Reserves that limit resource extraction can have many beneficial effects on populations of marine species, including increases in recruitment, abundance, individual animal size and overall biomass (Barrett et al. 2007; Tetreault and Ambrose 2007; Harmelin-Vivien et al. 2008; Lester and Halpern 2008). Increases in recruitment and abundance within reserve boundaries may in turn lead to increases outside the reserve through larval dispersal and adult spillover effects (Roberts et al. 2001; Russ et al. 2003; Alcala et al. 2005; Francini-Filho and Moura 2008; Harmelin-Vivien et al. 2008). Reserves also provide opportunities to compare the structure of populations and species assemblages within reserves to areas where fishing has occurred (Schroeter et al. 2001; Francini-Filho and Moura 2008). Fishery-independent data collected in reserves provide the means to monitor natural trends in population abundance and to compare trends between fished and unfished areas for improved stock assessment (Hand et al. 2009; Barrett et al. 2007). Reserves are also an investment in an insurance policy against uncertainty in stock assessment and management, and against natural calamities.

There may also be costs associated with implementation of reserves. Those who are economically tied to fishing the species may be negatively impacted in the short term by reductions in the total biomass available for harvesting or spatial constraints imposed on where fishing can take place. Reserve implementation may require harvesters to explore new fishing grounds which can reduce productivity for a time. There is a direct cost to creating and maintaining reserves, including upfront costs of research, development, consultation, and management as technical designs are planned, tested and vetted and costs for monitoring, enforcing and managing the reserves once they are implemented.

Reserve design in marine spatial planning exercises must therefore weigh benefits as well as costs and be evaluated against a set of performance criteria that are logically linked to well-defined management objectives. The types of data needed to evaluate reserve design against specified performance criteria also require careful consideration especially as these determine the suitability of analytical tools for carrying out the evaluation. Thus, the suitability of alternative tools or proxies for designing fisheries closure area networks depends first and foremost on the management objectives and how these are articulated in an operational sense. For instance map-based approaches (e.g. habitat suitability models, MARXAN analyses) may be appropriate in cases when management objectives are expressed simply in terms of a target area to be incorporated into the network. Alternatively, more sophisticated simulation models that account for dynamic interactions between fisheries, populations, and environmental processes (e.g. ocean circulation) may be required when management objectives are expressed in terms of changes in the patterns of distribution or abundance of species. Thus, the amount and type of information needed for analysis of reserve design depends not only on the type of analysis to be carried out, but ultimately on the management objectives and performance criteria that will be used to judge reserve design success.

In British Columbia (BC) resource managers are requesting information and advice on methods and biologically-based criteria that can be used to develop a coastwide network of Fishery Closure Areas for low mobility, benthic, broadcast spawning invertebrates (sea cucumber, sea urchin, bivalves, etc.) for consideration as a management tool. For many of these commercially harvested species in BC, there is limited knowledge of their life history parameters, including survival, growth, reproduction and movement patterns. While commercial fisheries for invertebrates are assessed and managed using the precautionary approach (Hand et al. 2009), there remains a high level of uncertainty in assumptions made about the life history parameters

of these species, and an additional level of precaution, such as a Fishery Closure Area Network, could mitigate the associated risks.

Most research on the design of networks of reserves has focused on mobile fish species, whereas research on reserve design for sedentary benthic invertebrates is limited. The goal of this paper is to provide a set of tools that could be used independently or together, depending on management objectives, to aid researchers and resource managers in designing single species Fishery Closure Area Networks (FCANs) for sedentary benthic invertebrate in BC, Canada.

The objective of this paper is to describe and apply a set of quantitative tools that can be used to provide advice on the number, size and spacing of single-species fishery closure areas in a network. The tools we describe and apply build on software packages and programs (ArcGIS, RAMAS, R, GRIP) that are currently available and being applied to address a broad range of marine spatial planning objectives. Together these tools form key components of a simulator that couples four sub-models of habitat suitability, metapopulation dynamics, dispersal, and fisheries management. Habitat suitability and species density models are used to define the spatial structure of the metapopulation dynamics sub-model and to set the carrying capacity and initial abundances of each population. Discrete populations within the metapopulation are linked through a model of larval dispersal. Spatially-explicit fisheries management scenarios are then implemented to simulate their effects on the distribution and abundance patterns of the target species. A baseline model is developed using the best available data and information. Once the baseline model is defined, a comprehensive sensitivity analysis is used to explore the influence of alternative reserve designs on the ability to achieve management objectives while accounting for key sources of uncertainty.

These tools provide modeled information about a single species population, in a finite geographic area, that can be used to provide advice on the ability of differing FCAN designs to meet management objectives. The presented methods are a proof of concept on how these tools could be implemented in BC, including an example of how the analysis could be carried out for a species and/or area, to address a broad range of spatial management questions and fishing management objectives provided there are sufficient biological and environmental parameters available.

In our paper, we develop our models using data from the Giant Red Sea Cucumber (*Parastichopus californicus*). Currently, this species is of particular interest due to: its current commercial fisheries re-expansion after a prolonged research and development stage (Hand et al. 2009); increased interest from aquaculture developers (DFO 2014); First Nation concerns over re-expansion and increased harvesting within their territorial waters, and; managers having begun implementing a number of ad-hoc Fishery Closures Areas for *P. californicus*, selected on the basis of common-sense criteria, into the fishery's IFMP (Hand et al. 2009; Duprey et al. 2011; Duprey 2011; Duprey 2012; DFO 2012). Pacific Fishery Management Area (PFMA) 12, located between the northeast coast of Vancouver Island and the mainland (Figure 2-1), was used as a trial location for the presented methods and analysis. This location was chosen due to the large amount of environmental and biological data available for the area. PFMA 12 has been thoroughly studied by oceanographers and there is a large amount of high resolution modeled environmental data for the area, including data that could be used to simulate larval dispersal. There have also been 4 sea cucumber surveys completed in the area (Hand et al. 2009; Duprey 2012; N. Duprey, Fisheries and Oceans Canada, Nanaimo, BC, unpublished data). Advice is not being provided for the creation of FCANs in PFMA 12, but rather methods, analytical techniques and the form simulator outputs could take are described in order to provide managers with a set of tools that could be used in developing FCANs, should this approach be implemented in BC.

Section 2 presents the development of two tools, models that predict the distribution and density of *P. californicus*. Models were developed using boosted regression tree (BRT) analysis, and the environmental and survey data available in PFMA 12. The results of these two models provide important inputs into the simulation tool used to explore various FCAN design scenarios, described in Section 3.

Section 3 presents a simulation model that explores the ability of differing FCAN designs to meet conservation and management objectives under current management practices. The simulation tool is a habitat-based, spatially explicit metapopulation dynamics model that comprises four coupled sub-models of habitat suitability, dispersal, meta-population dynamics and fisheries management, as well as the functions that link these four sub-components. Such models are increasingly used to assess species status, prioritize research, evaluate threats, and inform spatial management decisions for a broad range of species in terrestrial and aquatic systems (Akçakaya et al. 2004; Naujokaitis-Lewis et al. 2009; Pe'er et al. 2013). In our case study of *P. californicus*, we use the simulation model to evaluate FCAN design in terms of its ability to maintain population abundances above the limit reference point over a 100 year time frame.

The set of tools developed in Sections 2 and 3 thus include:

- code to develop spatially-explicit predictions of the location of suitable habitat and densities
- customized code to run, analyze and interpret boosted regression trees
- code to build baseline models of metapopulation dynamics models linked to habitat suitability, dispersal and fisheries management models
- customized code to run sensitivity analyses of baseline models
- code to collate, analyze and interpret simulation results of interest and evaluate reserve design against performance criteria

In section 4 we conclude by discussing the benefits, disadvantages, implications and requirements of using the presented tool to provide guidance on FCAN design. Future research needs, data requirements, and restrictions on how the model results can be interpreted will also be discussed.

2. PREDICTED HABITAT SUITABILITY AND DENSITY MODELS

2.1. INTRODUCTION

Knowledge of the location and density of a target species is important when creating a Fishery Closure Area Network (FCAN). However, the geographic coverage of survey data for most benthic invertebrate species currently targeted by commercial fisheries in British Columbia (BC) is limited. In order to fill this gap in areas that have not been surveyed, habitat suitability and density models can be used to estimate the probable distribution and density of a species in an area.

Pacific Fishery Management Area (PFMA) 12, was selected as the study area in this analysis as it has been relatively well surveyed for *Parastichopus californicus* relative to other areas of the coast. However, of the 48 Subareas in PFMA 12, 33 (69%) have not been surveyed. In order to create effective FCANs information on the likely distribution and density of *P. californicus* in areas that have not been surveyed is required.

Species distribution models (SDMs) can help meet science and management needs for conservation and planning by filling in information gaps related to the distribution and density of

species. SDMs use algorithms to predict the distribution or density of a species by relating occurrence or abundance data to background environmental data. SDMs can inform science and policy decisions by providing rapid and cost-effective methods for mapping and predicting suitable habitat for vulnerable species, important areas in the life history of fish, forecasting the invasion potential of non-indigenous species, and identifying candidates for protected areas. SDMs can also identify gaps in knowledge, thereby focusing research and exploration to maximize the utility of future effort and funding.

There are a wide variety of SDMs currently available. Boosted regression trees (BRT) are a relatively new machine learning modeling technique used to predict relationships between predictors (in this case environmental data) and response variables (biological survey data). Though BRT analysis is a relatively new technique, it has shown a great deal of promise. In a large study comparing models using presence-only data BRT produced some of the best predictive models (Elith et al. 2006). BRT analysis has also been used to predict the distribution of several freshwater and marine species. For example, it has been used to analyze trawl data to model the distribution of demersal fish species richness in the waters around New Zealand (Leathwick et al. 2006); to model the distribution of 15 diadromous and 15 non-diadromous fish species in New Zealand to examine the relationship between diadromy and dispersal ability (Leathwick et al. 2006a); and to predict the distribution of 96 species of demersal fish species using catch data from research trawls in support of marine protected area network planning (Leathwick et al. 2006b). BRT analysis was chosen based on these successful analyses (Leatherwick et al. 2006, 2006a, b) and its strong showing in comparative model assessments (Elith et al. 2006).

In the following section we use BRT analysis to predict areas of suitable habitat for *P. californicus* in PFMA 12, and to estimate density in each patch.

2.2. METHODS

2.2.1. Study area

The study area used for the predicted habitat suitability and predicted density models includes PFMAs 12 and 13. These areas are roughly bounded by Cape Scott in the west, Shelter Bay in the north, and Middlenatch Island in the south and east (Figure 2-1). The analyses were expanded to include PFMA 13 for two reasons: firstly, to increase the amount of sea cucumber survey data, as a large sea cucumber survey of PFMA 13 was conducted in 2008; secondly, to provide a better diversity of geographic locations and environmental conditions used in the predictive modelling. However, only the results from PFMA 12 are considered in subsequent metapopulation analysis (see Section 3).

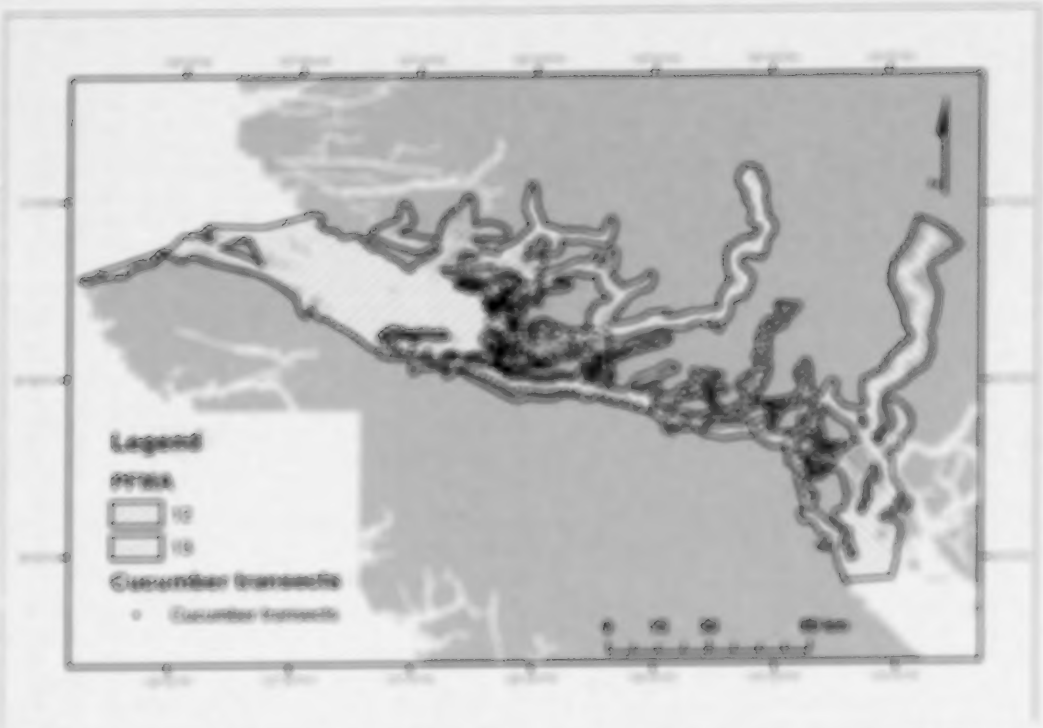

Figure 2-1. Study area for habitat suitability and density modelling. The area covers Pacific Fishery Management Areas (PFMAs) 12 and 13.

2.2.2. Sea cucumber survey data

Data on sea cucumber presence and density were obtained from surveys conducted in PFMA 12 and 13 by Fisheries and Oceans Canada (DFO) and the Pacific Sea Cucumber Harvesters Association (PSCHA) between 2008 and 2010 (Dupreey 2012, N. Dupreey, Fisheries and Oceans Canada, Nanaimo, BC, unpublished data). Surveys were only included in the analysis if they had been conducted in previously unfished areas, or areas that had not received commercial fishing pressure since 1997. In total, 526 transects from three different surveys were used (Table 2-1). Each transect was only surveyed once. Latitude and longitude coordinates of each transect were obtained from the deep point of the survey (typically around 15 m depth). When the deep coordinates were unavailable, the shallow water coordinates were used. The depth value used in the analysis was obtained from the depth layer described below, rather than the depth recorded on the survey. These surveys were used to determine the presence or absence of sea cucumbers, as well as the density (sea cucumbers/m^2). The density of sea cucumbers on each transect was calculated by dividing the total number of individuals observed by the total area surveyed. Transects were not truncated by the low tide line, though this should be completed in future analysis for species that do not inhabit intertidal waters.

Table 2-1. The Pacific Fishery Management Area (PFMA), survey year, and number of transects in each of the Parastichopus californicus surveys included in the predictive modeling. Transects were placed 2km apart in 2010 and 4 km apart in 2008 and 2009.

Survey Name	PFMA	PFM Subareas	Year	Number of Transects
Johnstone Strait	12	1, 2, 22, 23, 24	2009	47
Area 12 South Broughton	12	6, 26, 38, 39	2009	210
Area 12 Scintula	12	3, 4, 5, 18, 19, 21	2010	116
Johnstone Strait	13	7, 8, 9, 10, 11, 24, 25, 26, 27, 28, 31, 32, 33, 35, 36, 37, 39, 39, 40, 41, 42, 43	2009	152
Total				525

2.2.3. Environmental data

Decisions regarding which environmental variables to include were made based on ecological relevance and data availability. Spatially explicit data were collated for depth, chlorophyll *a* bloom frequency, bottom tidal speed, summer and winter values for bottom non-tidal current velocities, and spring, summer, fall, winter, minimum, maximum and range values for temperature and salinity. Some variables which are likely to be important predictors of the distribution and density of cucumbers, such as bottom type, fetch and exposure, could not be included because they were not available for the study area. Data were provided as 100 m by 100 m rasters (depth and chlorophyll *a* bloom frequency) and as a finite element grid with variable resolution ranging from about 100 m in narrow coastal channels to 8.5 km in open areas in the straits (all other data). The median distance between points in the finite element grid was 313.5 m. The data were imported into ArcMap 10.0 and interpolated to a 300 m by 300 m raster using the natural neighbour tool in the Spatial Analyst extension. The 300 m by 300 m grid was selected based on the original resolution of the data and biological relevance for *P. californicus*. The natural neighbour technique works by drawing Thiessen polygons around each input point. The natural neighbour algorithm identifies the nearest set of input points to a given query point (in this case, the center of the 300 m by 300 m raster cell) and interpolates a value weighted by the proportion of each associated Thiessen polygon (Sibson 1981). Land barriers were not considered during the interpolation process due to computational challenges; instead, land was clipped out of the raster once the interpolation had been completed. The years, sources and original resolution of environmental data used in this study are discussed below, and summarized in Table 2-2. The range and mean of each environmental variable across the study area and at locations where cucumbers were sampled is also summarized in Table 2-2.

Depth may play a role in determining the distribution and density of *P. californicus*. Densities of *P. californicus* have been shown to be lower at deeper depths in Sitka Sound, Alaska, USA (Woodby et al. 2009). However, another study in southeastern Alaska found that densities at depth ranges of 100-152 m can be as high as or higher than shallow water densities (Zhou and Shirley 1996). Through SCUBA and small submersible surveys, both studies found a preference for hard substrates with rock walls, crushed shell and gravel being the preferred

substrate (Chew and Shirley 1966; Mondloy et al. 2001). It is possible that results indicating that densities are lower in deeper water may be influenced by substrate type as soft substrates such as sand and mud are found in greater proportions at deeper depths. It is expected that the *P. californicus* exhibit a similar trend with some pockets of animals found in deeper water, but a majority of the population inhabiting water depths <30 m (Hand et al. 2009). This depth layer was obtained as a 100 m by 100 m raster grid (Edward Gregr, unpublished data, Scitech Environmental Consulting, Vancouver, BC, pers comm.). This layer was derived from source data from the Living Oceans Society (~2m) and the National Oceanic and Atmospheric Administration (NOAA, 200m).

Chlorophyll *a* bloom frequency may be an indicator and measure of productivity in the area. The chlorophyll *a* bloom frequency layer was obtained as a 100 m by 100 m raster grid, though original resolution for the data was 1000 m (Edward Gregr, unpublished data, Scitech Environmental Consulting, Vancouver, BC, unpublished data, pers comm.). Data for this layer were derived from the algal 1 band from the Medium Resolution Imaging Spectrometer (MERIS) instrument on the European Space Agency ENVIronmental SATellite (ENVISAT) platform for the years 2007-2011. The monthly bloom frequency was calculated by counting the number of months in the spring (defined as March 15 – June 21) when the average concentration of chlorophyll *a* was greater than 2.3 mg/m^3. Values range from 3 (no spring blooms in the 3 year period) to 33 (blooms every month in the spring in the 3 year period).

Current and tidal speed may influence the distribution and density of *P. californicus*. Areas of strong currents and high exposure result in lower sea cucumber abundance, as do areas that are highly protected (Hand et al. 2009). It appears the population prefers neither extreme, likely because strong currents negatively affect the deposition and increase energy costs when living in the substrate and during locomotion, while very low currents do not bring sufficient nutrient exchange into the habitat. Average summer and winter values for bottom non-tidal current speed, bottom tidal speed and spring, summer, fall, winter, minimum, maximum and range values for bottom salinity and temperature were obtained from a well-validated tidal circulation model of the eastern North Pacific (Foreman et al. 2009). Data were obtained directly from the senior author of that paper (Mike Foreman, Institute of Ocean Sciences, Sydney, BC, pers comm.). All data were provided in a finite element grid with variable resolution.

Salinity is likely to play a role in the distribution and density of *P. californicus*. Echinoderms are considered stenohaline, meaning they generally cannot tolerate wide fluctuations in salinity (Dickie and Diehl 1987). The study area has several large inlets that are fed by rivers, resulting in a large range of salinity values throughout the study area and the year (see Table 2-2). There is currently no published data specifically on the effects of changes in salinity on *P. californicus*, however studies done on the sea cucumber *Apostichopus japonicus* have shown that changes in salinity can affect the behaviour, development and survival of larvae (Kashenko 2000), can cause mortality in juveniles (Wang et al. 2011), and can reduce the growth rate of adults (Yuan et al. 2010). It is therefore likely that salinity will play a role in the distribution and density of *P. californicus*.

Temperature is known to affect the growth and survival of several holothurian species (Ayala and Ahuatzin 2003; Dong et al. 2006; Zamora and Jeffs 2011). For example, juvenile *Isostichopus nolitis* had gradually declining daily growth rates when temperatures moved from 12 C to 18 C to 21 C (Zamora and Jeffs 2011). Currently there is no published data on the effects of changes in temperature on *P. californicus* growth or survival. However, we assume that *P. californicus* does have a preferred temperature range for optimal growth and survival and that populations found outside of these ranges will be at a disadvantage. It is therefore expected that temperature will play an important role in the distribution of *P.*

californicus at local scales, but the importance of this variable may be more difficult to ascertain when large geographic ranges are used.

Table 2-2. Summary of type, source, resolution, range and mean (in brackets) of values of environmental data used in the habitat suitability modeling. The depth and chlorophyll a bloom frequency were obtained from E. Gregr (SciTech Consulting). All other layers were obtained from M. Foreman.

Variable	Original resolution	Study area range (mean)	Sampled range (mean)
Depth (m)	100 m	1 – 650 (145)	1 – 153 (15)
Chlorophyll *a* bloom frequency	1200 m	3 -20 (19.7)	3 – 16 (7.5)
Bottom tidal speed (m/s)	100 m – 8.5 km	0.001 – 1.70 (0.073)	0.002 – 0.48 (0.060)
Bottom current speed (m/s)	100 m – 8.5 km	-	-
Summer		0.0002 – 4.36 (0.13)	0.0005 – 1.53 (0.068)
Winter		0.0005 – 2.93 (0.10)	0.0008 – 2.72 (0.090)
Bottom temperature (°C)	100 m – 8.5 km	-	-
Spring		6.54 – 13.29 (8.46)	7.92 – 11.49 (9.43)
Summer		6.28 – 15.82 (9.19)	8.57 – 12.86 (10.73)
Fall		5.57 – 10.93 (8.51)	6.14 – 9.62 (8.60)
Winter		6.16 – 9.02 (7.60)	6.65 – 7.77 (7.23)
Minimum		5.57 – 8.69 (7.52)	6.14 – 7.77 (7.23)
Maximum		7.09 – 15.82 (9.38)	8.57 – 12.86 (10.73)
Range		0.07 – 8.77 (1.86)	1.22 – 5.89 (3.51)
Bottom salinity (psu)	100 m – 8.5 km	-	-
Spring		2.45 – 33.69 (29.76)	8.15 – 31.39 (27.19)
Summer		1.39 – 33.66 (29.78)	6.94 – 31.87 (26.65)
Fall		13.64 – 33.39 (30.31)	19.30 – 31.56 (28.47)
Winter		19.51 – 32.93 (30.47)	26.46 – 31.09 (29.67)
Minimum		1.39 – 32.34 (29.24)	6.94 – 31.09 (26.55)
Maximum		19.51 – 33.70 (30.96)	26.46 – 31.87 (29.77)
Range		0.03 – 20.95 (1.71)	0.11 – 19.54 (3.22)

2.2.4. Boosted regression tree (BRT) analysis

BRT is a machine learning modeling technique used to quantify relationships between predictors and a response. Machine learning techniques differ from traditional statistical approaches in that they use algorithms that learn the relationship between a response (in this case the presence or absence of a species and/or its density) and its predictors (in this case environmental variables) (Breiman 2001) rather than having an *a priori* assumption about the relationship between the predictors and the response. BRT analysis combines two algorithms:

1. "regression trees", single models that partition predictors using a series of rules that maximizes the homogeneity of the response data; and
2. "boosting", a method for developing several models and combining them (Friedman et al. 2000).

Regression trees have several advantages, including their ability to use any type of data (numeric, binary, categorical, etc.), their insensitivity to outliers, and their accommodation of missing data in predictor variables. However, regression trees have difficulty modeling smooth functions, and are very sensitive to small changes in the training data. Boosting makes it possible to model complex response surfaces and helps overcome the inaccuracies of a single model. The boosting algorithm calls the regression tree algorithm repeatedly, every time weighting the data differently so that records that were misclassified in the last round are emphasized. The model is fitted in a forward, stepwise fashion until it eventually overfits the data (Elith et al. 2008). The optimal number of trees in the boosted model is chosen by measuring prediction accuracy on independent data.

Two separate models were constructed to predict the suitability of habitat for sea cucumbers, and the density of sea cucumber populations in the study area. Habitat suitability was predicted using the observed presence or absence of *P. californicus* (represented by 1 and 0, respectively) as the response variable. Presence/absence data were fit with a Bernoulli distribution. The observed spatial density of *P. californicus* (in sea cucumbers/m^2) was used as the response variable in the density model. Data were fit using a Gaussian distribution. All models, including those built for the parameter tuning and sensitivity analyses were built and analysed in R (R Development Core Team 2011) version 2.14.1 using the packages *gbm* version 1.6-3.2 (Ridgeway 2012) and *dismo* version 0.7-17 (Hijmans et al. 2012). Raster layers of results were created using the R packages *raster* version 2.0-08 (Hijmans and van Etten 2012), and *rgdal* version 0.7-12 (Keitt et al. 2012).

2.2.5. Parameter tuning

As with any predictive modeling, if a model is overfit to the training data it is less able to provide good predictions with new data. Regularization methods are used to control the degree to which a model is fit to the data and to find a balance between model fit and predictive capability (Hastie et al. 2001). With BRT, regularization is particularly important, as the algorithm allows the model to completely overfit training data. In BRT, overfitting is controlled by introducing stochasticity, and by optimizing the number of trees used to construct the model (*nt*).

Stochasticity is implemented in BRT models by only using a random selection of the training data at each step in model building. The proportion of data used at each step is known as the bag fraction (*bf*). For example, a *bf* of 0.75 would mean that at each step in the model building process 75% of the available data are selected at random (without replacement) for use. Optimal bag fractions will vary depending on the data used.

In addition to adding stochasticity, the number of trees (*nt*) used to construct a BRT model will also influence the degree to which a model is fit, with larger numbers of trees being more likely

to overfit data. As a rule of thumb, Elith et al. (2008) recommend fitting models with at least 1000 trees. In BRT, *nt* is determined by a combination of the learning rate, *lr*, and tree complexity, *tc*. The *lr*, also known as the shrinkage parameter, reduces the contribution of each tree as it is added to the model. Smaller *lr* values will cause the model to grow more slowly, and will result in larger numbers of trees being required. Tree complexity, *tc*, indicates the number of nodes or splits in each tree, and controls whether or not interactions between predictors are fitted. Fitting trees with a larger number of nodes reduces the total number of trees required to minimize error.

In the present analysis, parameter tuning was conducted separately for both the habitat suitability and density models to find optimum values for *bf*, *lr*, and *tc* so as to reduce overfitting and minimize predictive error. Several values were tested for *bf* (0.25, 0.5, 0.6, 0.75, 0.9), *lr* (0.01, 0.005, 0.001, 0.0005), and *tc* (1, 2, 3, 5, 7, 10), and were based on ranges used by Elith et al. (2008). All possible combinations of *bf*, *lr*, and *tc* were tested (120 iterations) to determine the combination that minimized overall predictive error.

The cross-validation method built into the R package dismo (Hijmans et al. 2012) was used to evaluate the predictive performance of each combination of parameters. Essentially, cross-validation works by partitioning available data into subsets (in this case 10). These subsets are then used to create 10 unique sets of training data, consisting of a unique combination of 9 of the 10 subsets, with a corresponding test data set (the remaining subset). The 10 training data sets are used to simultaneously build BRT models (using the defined values for *bf*, *lr*, and *tc*) with a given number of trees. The *nt* is systematically increased and predictive performance is recorded until the minimum predictive error (measured by deviance), and thus the optimal *nt*, is found. In this analysis, predictive error was measured by deviance. Deviance is calculated as two times the log-likelihood (Gelman et al. 2003) with smaller values indicating better fit. A final BRT model is then built using all available data and the optimal *nt*. Even though a final model was built with all available data, the performance of each combination of tuning parameters was evaluated using the mean deviance of the 10 cross validation models with the optimal *nt*. Performance of the final models for predicted habitat suitability and density is reported using the area-under-the-curve (AUC) of the receiver-operator characteristic (ROC) of the cross validation models and the percent density explained (PDE), respectively, as they are clearer and more representative descriptors of model performance. The AUC is a measure of predictive accuracy and can have values ranging from 1, indicating perfect distinction between presence and absence to 0.5, indicating a model is no better than random. In this analysis, PDE compares the null deviance in the input abundance data with residual deviance in the cross-validated input abundance data in relation to cross-validated modelled predictions. PDE is calculated as:

$$\frac{\textit{(null deviance - cross-validated residual deviance)}}{\textit{null deviance}} \times 100$$

2.2.6. Sensitivity analyses

A number of sensitivity analyses were performed to test the habitat suitability and density models' sensitivity to spatial resolution, depth, and the influence of correlated and modelled data. In addition to the base case scenario using a 300 m-by-300 m grid, models were built using 600 m and 1200 m grids to determine whether finer scale information improved the performance of models. Sensitivity to depth was tested by limiting the analysis to areas shallower than 30 m depth (the base case used the full depth range within study area), and by removing depth from the analysis. Sensitivity to correlation among environmental variables was tested by sequentially examining each environmental layer and, where applicable, removing all other variables that were either moderately correlated (Pearson's $r \geq 0.75$), or highly correlated (Pearson's $r \geq 0.9$).

Six of the 19 environmental layers (bathymetry, spring chlorophyll *a* bloom frequency, summer and winter current speed, tidal speed and fall temperature) did not have a Pearson's $r \geq 0.75$ with any other layers, and winter and minimum temperature did not have a Pearson's $r \geq 0.9$ with any other layers. A total of 24 sets of environmental data layers were created for the correlation sensitivity analysis. Potential sensitivity to modelled data was tested by removing all modelled data (tidal and current speeds, temperature and salinity), and only temperature and salinity. All models built for the habitat suitability and density sensitivity analyses, including the base case scenarios, used the optimum parameter values identified in the parameter tuning. As with the parameter tuning, cross validation (10 partitions) was used to assess the average performance of each sensitivity run. The deviance of the resulting models were compared using a two-sided Wilcox exact rank sum test implemented using the *exactRankTests* version 0.8-22 (Hothorn and Hornik 2011) package in R.

2.2.7. Sensitivity analyses

Spatial autocorrelation in the model residuals for both the probability and density SDMs was tested for using Moran's *I* (Moran 1950), implemented in the R package *raster* package (version 2.0-08, Hijmans and van Etten 2012). Moran's *I* ranges from -1 (perfect dispersion) to 1 (perfect correlation), with 0 representing a random spatial distribution.

2.3. RESULTS

2.3.1. Sea cucumber data

Sea cucumbers were observed on 433 (82.3%) transects used in this analysis. At sites where cucumbers were observed, there was a minimum density of 0.0021 sea cucumbers per square meter (sc/m^2), a maximum density of 0.83 sc/m^2, and a mean and median of 0.16 sc/m^2 and 0.11 sc/m^2, respectively.

2.3.2. Parameter tuning

Deviance was used to evaluate the predictive performance of the models built during the parameter tuning. Values for deviance ranged from 0.877 to 0.931 for the habitat suitability model, and 0.0220 to 0.0235 for the density model. Values for AUC in the habitat suitability model ranged from 0.575 to 0.686. Values for PDE in the density model ranged from 3.8% to 10.2%. Both models passed the threshold of at least 1000 trees (Table 2-3) suggested as a rule of thumb by Elith et al. (2008). Values for *lr*, *tc*, *bf*, and *nt* for optimal predictive performance, as well as AUC and PDE are summarized in Table 2-3.

Table 2-3. Optimal parameter values for learning rate (lr), tree complexity (tc) and bag fraction (bf), AUC (with standard error, SE, in brackets), percent deviance explained (PDE) and the number of trees for the best performing models in the tuning for habitat suitability and density BRT models.

Model	Parameters		AUC (SE)	PDE	Num. of trees (*nt*)
Habitat suitability	*lr*	0.005	0.635 (0.0327)	NA	1040
	tc	3			
	bf	0.9			
Density	*lr*	0.005	NA	10.2 %	1650
	tc	7			
	bf	0.25			

2.3.3. Sensitivity analysis

Models of both the distribution and density of *P. californicus* were insensitive to variations in grid size, restriction or elimination of depth, the removal of correlated variables, and the removal of modelled data. Model performance, as measured by deviance, of each of the 30 different sensitivity runs for both habitat suitability and density was not significantly different ($p > 0.05$) than the base case scenario.

2.3.4. Boosted regression tree results

2.3.4.1. Contribution of Variables

The relative contribution of environmental variables was calculated in the R package gbm using formulae developed by Friedman (2001). Calculations are based on the number of times a variable is selected for splitting and the improvement to the model caused by each split (Friedman and Meulman 2003). Variable contributions are scaled to 100 so that they can be reported as percent contribution.

The exact contribution of each environmental variable differed between the predicted habitat suitability and predicted density models (Figure 2-2), though they shared similar trends; the top six and the bottom three variables were the same in both models. Tidal current speed was the most important predictor of habitat suitability (14.38%) and sea cucumber density (10.66%). Fall and winter temperature, summer and winter current speed and depth are the next five most important variables in both models. Combined, the top six variables contributed 54.97% to the habitat suitability model, and 54.52% to the density model. On the other end of the spectrum, minimum salinity and minimum and maximum temperature contributed relatively little to the models. Tidal current speed, spring and fall temperature and fall salinity were relatively more important in the suitability model than they were in the density model. Spring, winter, range and minimum salinity values as well as summer and range of temperature values were relatively more important in the density model than they were in the suitability model.

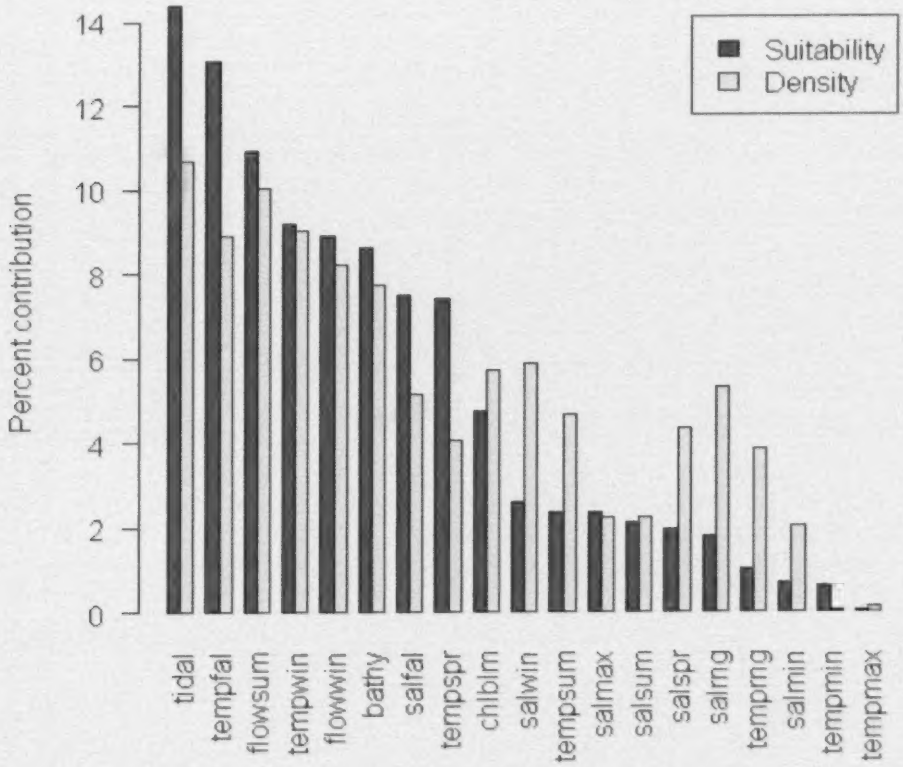

Figure 2-2. The percent contribution of each environmental variable to the predicted habitat suitability model (black bars) and the predicted density model (white bars).

2.3.4.2. Fitted Function Plots

Fitted function plots produced from a BRT model provide a visual representation of the effect a predictor variable has on a response after all of the effects of other variables have been taken into account (Elith et al. 2008). They are not perfect representations of the relationship, especially if there are a number of interactions between variables or they are highly correlated. However, they do provide information on the relationship between the predictor and response.

Tidal speed

Tidal speed was identified as the most important environmental predictor, contributing 14.4% and 10.7 % to models of habitat suitability and density, respectively (Figure 2-2). When the tidal speed is close to 0 m/s it has a slightly negative influence on both habitat suitability and density (Figure 2-3 and Figure 2-4). This changes to a positive effect once tidal speeds reach about 0.02 m/s. In the habitat suitability model this influence plateaus until tidal speed reaches approximately 0.2 m/s, at which point tidal speed has a negative effect on habitat suitability. In the density model the positive relationship changes when speeds reach approximately 0.1 m/s, at which point tidal speed has little influence on density.

Fall temperature

Fall temperature was the second most important variable for the habitat suitability model, and the fourth most important variable for the density model, contributing 13% and 8.9% to the

models, respectively (Figure 2-2). Fall temperature has a similar effect in both models (Figure 2-3 and Figure 2-4). There is a slight positive effect on predictions for temperatures up to about 8 C, at which point the positive effect becomes stronger. The relationship becomes slightly negative at around 9 °C for habitat suitability, and 8.5 °C for density.

Summer non-tidal current speed

Summer non-tidal current speed is the third and second most influential variable in the models of habitat suitability and density, contributing 10.9 and 10% to the models, respectively (Figure 2-2). It has a similar influence in both models (Figure 2-3 and Figure 2-4). Low current speeds have a slightly negative effect on predictions of habitat suitability and density. This effect diminishes as speeds reach approximately 0.25 m/s, at which point summer non-tidal current speeds have no influence on the responses.

Winter temperature

Winter temperature is the fourth most influential predictor of habitat suitability (9.2%), and the third most important predictor of density (9%)(Figure 2-2), though it influences the models slightly differently (Figure 2-3 and Figure 2-4). Temperatures below approximately 7.2 °C have a slightly negative influence on habitat suitability. Above 7.2 °C there is a positive relationship between increasing temperatures and habitat suitability, within the range observed. For density the opposite is true: temperatures below approximately 7.2 °C have a slightly positive influence on density, but warmer temperatures have a negative effect.

Winter non-tidal current speed

Winter non-tidal current speed is the fifth most important predictor in both models, contributing 8.9% and 8.2% of information in the habitat suitability and density models, respectively (Figure 2-2). Current speeds around 0 m/s have a negative effect on both responses. This effect diminishes as speeds increase to about 0.1 and 0.25 m/s for habitat suitability and density, respectively (Figure 2-3 and Figure 2-4).

Depth

Depth is the sixth most important predictor of habitat suitability and density, contributing 8.6% and 7.7% to the respective models (Figure 2-2) Depths at or close to 0 m had a negative effect on both predicted habitat suitability and density (Figure 2-3 and Figure 2-4). The relationship between both responses diminishes as depth increases before the influence plateaus at about 25 m for habitat suitability, and 50 m for density.

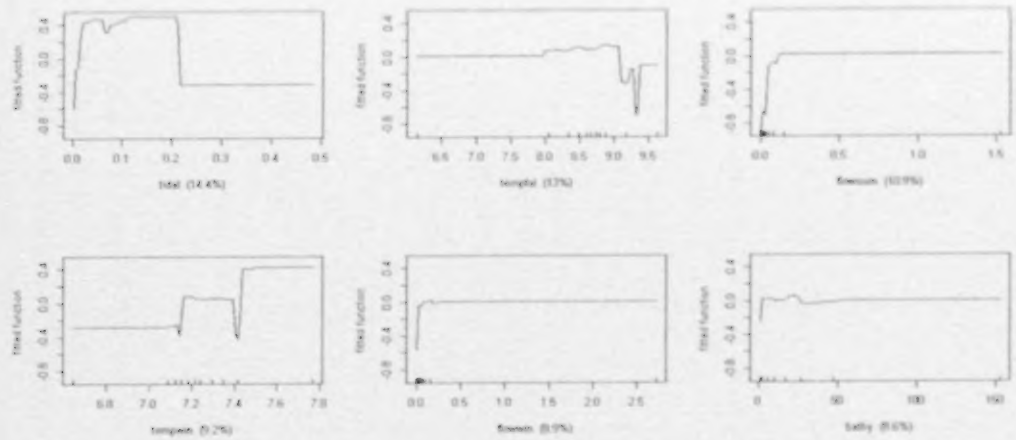

Figure 2-3. Fitted function plots for the top six most influential variables for the predicted habitat suitability model. (Top row of graphs from left to right: Tidal current speed; and temperature fall; summer current. Bottom row of graphs from left to right: temperature winter; winter current; and bathymetry).

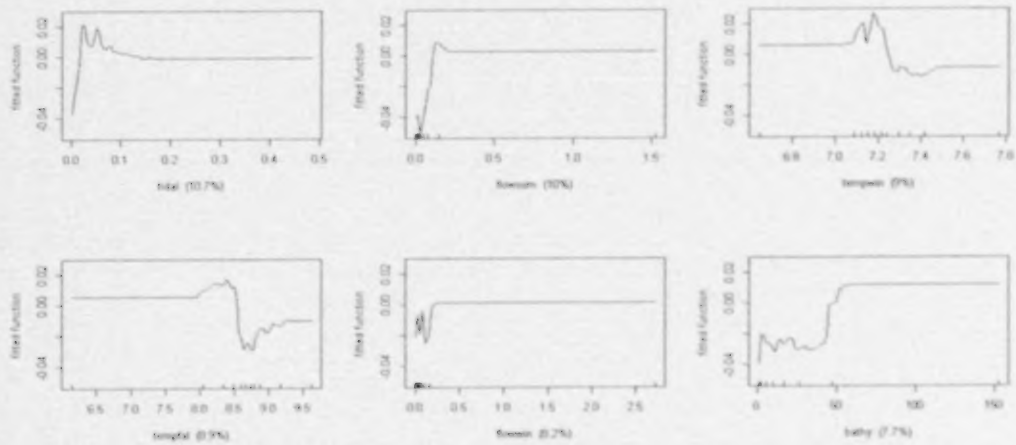

Figure 2-4. Fitted function plots for the top six most influential variables for predicted density model. (Top row of graphs from left to right: tidal current speed; temperature summer; and temperature winter. Bottom row of graphs from left to right: temperature fall; summer current; and bathymetry).

2.3.4.3. Predicted habitat suitability

Results of the predicted habitat suitability model are provided on a gradient ranging from 0 to 1, where 0 is completely unsuitable habitat, and 1 is perfectly suitable habitat. The results of the BRT modelling for predicted habitat suitability are presented in Figure 2-5. Predictions of habitat suitability are able to discriminate between observed presences and observed absences (Figure 2-6). When the purpose of modelling is to identify areas of potential habitat for a species, as in the current study, a threshold is usually chosen to distinguish between areas predicted to have sea cucumbers (predicted suitable habitat) and areas predicted to not have sea cucumbers (predicted unsuitable habitat). In order to select a threshold, one must find a balance between the sensitivity (the true positive rate, or the ability to correctly identify presence), and the specificity (the true negative rate, or the ability to correctly identify absence)

of the model. The intuitive threshold of 0.5 may not always provide an ideal balance between sensitivity and specificity. For example, in the present modelling exercise a threshold of 0.5 results in a sensitivity of 0.995 and a specificity of 0.280. This means that the model is very good at correctly identifying presence (sensitivity), but is not very good at correctly identifying absence (specificity). In contrast, when the threshold is increased to 0.75 the sensitivity remains good (0.896), while the specificity increases substantially to 0.784.

A variety of methods can be used to identify thresholds. Thresholds should be dependent on the prevalence of the species, as model results are generally biased by prevalence (Jiménez-Valverde and Lobo 2007). The maximum sum of sensitivity-plus-specificity is linearly related to prevalence and has been shown to be quite accurate (Jiménez-Valverde and Lobo 2007). This method was therefore selected in the current analysis. The threshold was calculated using the PresenceAbsence package version 2.14.2 in R (Freeman and Moisen 2008). The maximum sum of sensitivity-plus-specificity was found to be 0.75. In Figure 2-5, areas predicted to have suitable habitat for *P. californicus* are coloured green, orange or red. The majority of the study area is predicted to be suitable habitat for *P. californicus* with the exception of a few areas, mainly at the heads of inlets, off the northern tip of Vancouver Island, and around Discovery Passage, Malcolm Island, and the Broughton Archipelago.

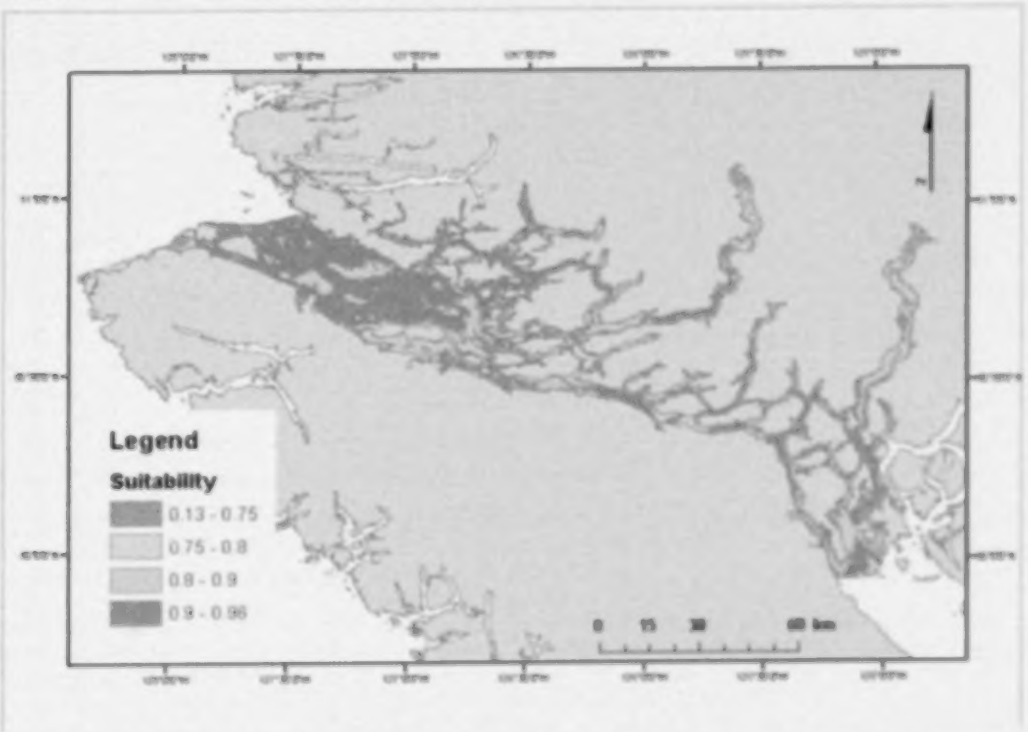

Figure 2-5. Boosted regression tree predictions of habitat suitability for Parastichopus californicus in Pacific Fishery Management Area 12. Areas in blue are predicted to be unsuitable habitat, while those that are green, orange or red are predicted to be suitable.

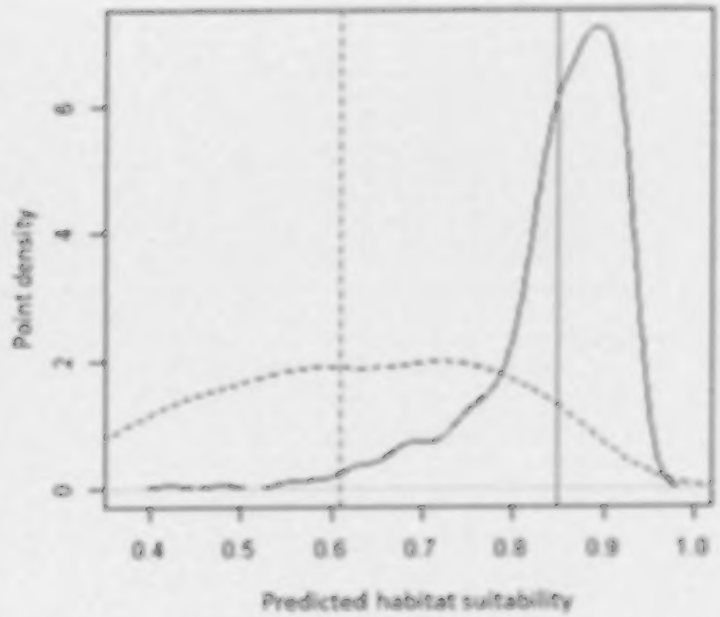

Figure 2-6. Density plot comparing predicted habitat suitability values and P. californicus observations from survey data. Predicted habitat suitability is on the x-axis; dotted lines represent observed absences and solid lines represent observed presences. Vertical lines indicate the mean. This plot indicates that the model is, on average, predicting a difference between observed presences and observed absences.

2.3.4.4. Predicted density

Results of the predicted sea cucumber density (sc/m^2) model are presented in Figure 2-7. Areas of higher density tend to be closer to shore and up in the inlets, though there are patches of higher predicted densities throughout Queen Charlotte Strait and Discovery Passage. The north coast of Vancouver Island, the area around Malcolm Island, Johnstone Strait, Bute Inlet, and the area between Quadra and Cortes Islands have large areas of predicted low densities.

There is a linear relationship between the observed densities of sea cucumbers and the predicted densities (Figure 2-8), however it is not the ideal one-to-one relationship. When observed densities are high the predicted values tend to be lower than the observed values and when observed densities are low the model results tend to over-estimate density.

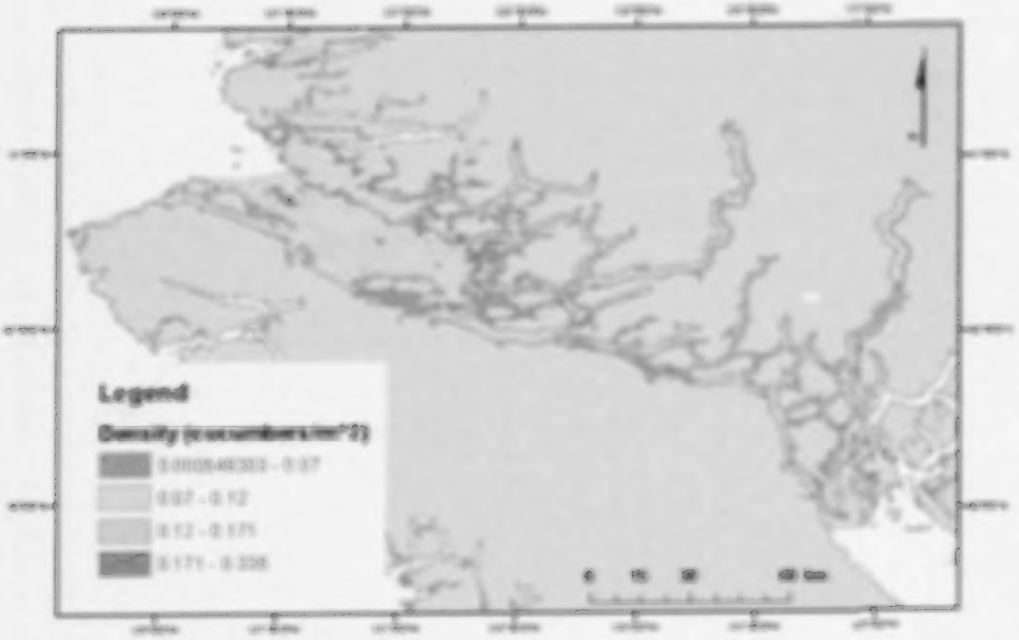

Figure 2-7. Boosted regression tree predictions of sea cucumber density (ind/m^2). Cutpoints are divided into quartiles of the predicted density.

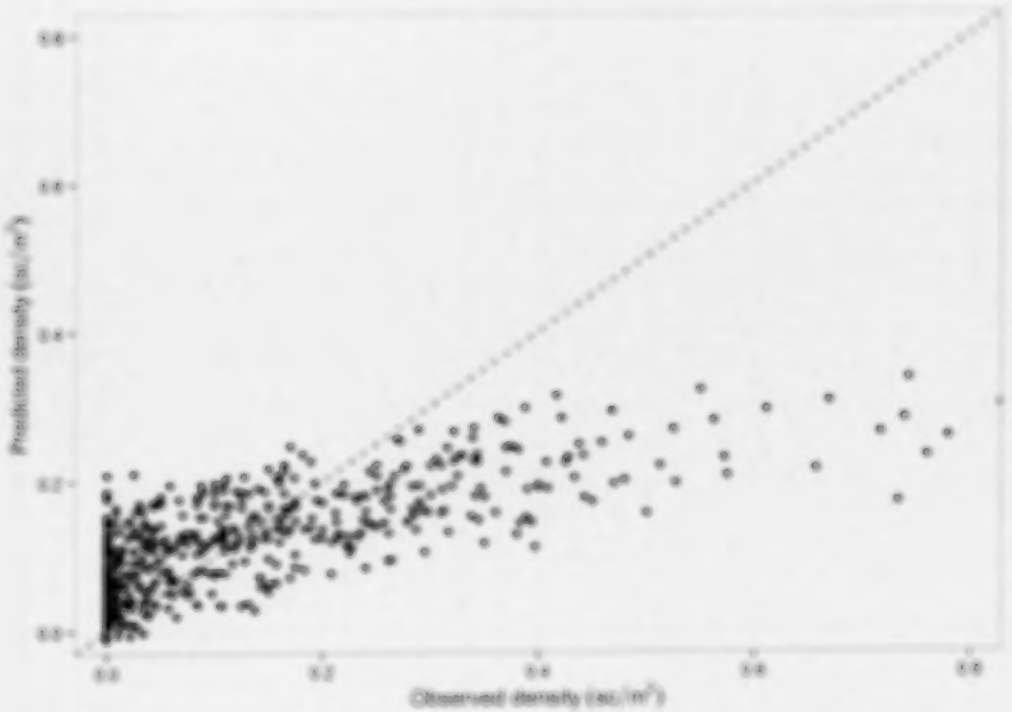

Figure 2-8. Plot comparing the observed (x-axis) and predicted (y-axis) spatial density of sea cucumbers per square meter (ea/m²). The dashed line indicates a one-to-one relationship.

2.3.5. Spatial autocorrelation

The model residuals for the probability SDM had Moran's *I* = 0.111, while the density SDM had Moran's *I* = 0.107. These results suggest that spatial autocorrelation is not an issue in these analyses.

2.4. DISCUSSION

Section 2 presented a demonstration of BRT modelling and its use in predicting the distribution and density of low-mobility benthic invertebrates. In this section we provide a discussion of the results of the models of predicted habitat suitability and density, the interplay between those models, the influence of key environmental predictors, the limitations and uncertainties associated with this type of analysis, and a description of how these models can be used in the context of developing an FCAN.

2.4.1. Sensitivity analysis

Both evaluation techniques and threshold selection have been evolving in the literature recently. Future applications of this method should evaluate the consequences of type 1 and type 2 errors in their analysis, review recent literature on the subject, and select the most appropriate methods. The relative prevalence of a species can also influence appropriate methods for both evaluating the model performance and threshold selection.

2.4.2. Habitat suitability

Results of the habitat suitability modelling predict that *P. californicus* is a generalist species and can be found throughout the study area. The main exceptions, where they are not predicted to be present, are the heads of many of the larger inlets. These distribution patterns are consistent with our knowledge of the distribution of the species. They have been seen throughout the coast in a variety of habitats, though are less commonly seen at the heads of inlets (N. Duprey, personal observation). Many of the inlet heads in the study are subject to low tidal currents, which was associated with low abundance. Groundtruthing of the habitat suitability model in unsurveyed areas would help provide information on the validity of the results.

2.4.3. Density

Results of the BRT density model indicate that predicted density of *P. californicus* is not homogeneous, but varies throughout the study area. Generally, areas closer to shore and up in inlets tend to have higher predicted densities, though there are other patches with predicted high densities. There are several large patches where density is predicted to be low, most notably the north coast of Vancouver Island, the area around Malcolm Island, Johnstone Strait, Quite Inlet, and the area between Quadra and Cortes Islands. Model predictions of density seem to have a reasonable relationship with observed densities (Figure 2-8), and predictions of many of the areas of low density match our knowledge of the area. However, some of the predictions of higher density in unsurveyed areas, particularly at the heads of large inlets, do not match our understanding of the distribution of sea cucumbers from survey data. As mentioned in the habitat suitability section, *P. californicus* is not commonly seen at the heads of inlets (N. Duprey, pers. obs.). Additionally, the habitat suitability model does not predict those areas to have suitable habitat. This discrepancy does not necessarily mean that the density model is incorrect, but this result certainly warrants further investigation. As with the habitat suitability model, groundtruthing the density model would help validate results.

2.4.4. Interplay between the two models

The contrast between predictions of habitat suitability and density in the heads of large inlets highlights the importance of considering the interplay between the models of habitat suitability and density when forming conclusions about the distribution and density of the species. Areas may be predicted to be suitable, but may have low predicted densities, or the inverse may be true. Therefore, the two maps should not be considered in isolation, and other knowledge of the biology, distribution and density of the species must be considered.

2.4.5. Contribution of environmental variables

According to the BRT models developed in this analysis, the main drivers of the distribution and density of *P. californicus* can be grouped into three main categories:

1. water speed (tidal, and summer and winter current speeds);
2. temperature (fall and winter values); and
3. depth.

Of the six most influential variables in predicting the distribution and density of our study species, three related to water speed: tidal, summer current, and winter current speeds. The fitted function plots suggest that when values for these variables are close to zero, they have a negative influence on predicted habitat suitability and density. As the water speed increases the negative effect diminishes and becomes positive before an inflection point at speeds around

1.2 m/s. At that point water speed has very little influence, or in the case of total speed in the habitat suitability model, has a negative influence. This is consistent with our knowledge of habitat preferences of *P. californicus*. It seems that *P. californicus* does not prefer areas with very weak currents, nor do they inhabit areas with strong currents (Hamel et al. 2008).

Temperature, specifically fall and winter values, also appears to be influential in the predicted distribution and density of *P. californicus*. The fitted function plots indicate that *P. californicus* are more likely to be found, and in greater densities, in areas where the temperature is approximately 8 to 8.5 °C in the fall, and areas cooler than 7.2 °C in the winter. Studies by Zamora and Jeffs (2012) have shown temperature changes of 2 °C can affect the growth of sea cucumbers, so it is possible *P. californicus* preferentially inhabit areas within a certain temperature range. Further studies on the biology and physiology of this species of sea cucumber are needed to confirm whether or not the model results accurately reflect the temperature preferences of *P. californicus* in Areas 12 and 13.

Finally, depth was identified as an important predictor of the distribution and density of *P. californicus* in our study area. The influence of depth on the two responses modelled differed. Depths at or close to 0 m had a negative influence on both responses. As depth increases it begins to have a slightly positive effect on habitat suitability up to a depth of about 20 m at which point it is no longer very influential. In the density model depth continues to have a negative influence on density, although the influence diminishes, up to a depth of about 30 m, at which point it has a slightly positive influence. These results should be interpreted with caution as they may be biased by the depth restriction of the sea cucumber survey data used in the modelling exercise (<18 m; see Limitations and Uncertainty section below). Further research into the distribution and abundance of *P. californicus* below divable depths would likely benefit model predictions.

2.4.6. Limitations and uncertainty

While the model results correspond with much of our existing knowledge of the distribution and density of *P. californicus*, it is important to note some of the limitations of these types of models generally. Models, such as the one developed here, provide approximations of reality based on observations. These representations are not perfect, and the performance of these models can be highly influenced by the type and quality of input data used. Therefore it is important that the results be interpreted with a degree of caution.

One limitation of the model is the scale. Models should be built on a scale that is biologically relevant to the study species (generally based on range, size and mobility), that is appropriate for the available data (so that data are not extrapolated or interpolated too much), and on a scale that is computationally feasible. These factors do not always align, and sometimes trade-offs must be made. For example, if the study species is relatively small and immobile, a smaller grid size is more appropriate. However, environmental data may not be finely enough resolved for such a detailed map, or the study area may be so large that it is not computationally practical to operate on such a fine scale. In such cases the scale of the analysis needs to be done in such a way so as to balance the biological appropriateness, the resolution of data, and the size of the study area.

The existence of spatial autocorrelation in a model violates the assumption of independent and identically distributed residuals, and can result in an increase of type I error (false positives). There are several methods to account for spatial autocorrelation in SDMs (e.g., review by Dormann et al. 2007), including some specifically for use with BRT (Crase et al. 2012). However, these methods should only be applied in areas that have been sampled. Extrapolating results into areas that have not been sampled is not recommended, because the relationship between predictors and the modelled response may be different in other areas.

(Dormann et al. 2007). Therefore, at this time there are no appropriate methods to account for spatial autocorrelation in unsampled areas, though that may change as new techniques are developed. Spatial autocorrelation was not an issue in the present analysis. However, future analyses should continue to test for spatial autocorrelation because it may be an issue with different species or study areas.

One source of uncertainty is whether or not all influential environmental variables and/or ranges of the variables were captured and included in the analysis. In particular, the poor fit of the density model suggests that important environmental or other influential variables were not adequately captured. Obvious absences are the lack of bottom type and facies information. Studies in BC and Alaska have shown that *P. californicus* appears to have a habitat preference for hard substrates or mixed substrates (Campagna and Hand 1999; Zhou and Shirley 1996; Woodby et al. 2000). Bottom type would therefore likely be an important predictor of distribution and density. Unfortunately reliable bottom type and facies information is not available for much of the coast of BC, including the study area used here. Other variables that are likely to have a role in the distribution and density of a species, such as exposure, should be included when available and feasible. Additionally, sea cucumbers sampling may not have occurred throughout the entire ranges of the environmental variables found within the study area. Therefore extrapolation into un-sampled environmental variables ranges may pose a problem for predictions. The addition of these data may improve results of the models.

Along with missing environmental predictors, another potential source of bias is the biological data. In this study, stock assessment surveys of *P. californicus* were used to provide information on the responses modelled. These surveys are designed to provide good spatial coverage and assess the biomass of sea cucumbers within the most common fishable depths. Transects typically go to approximately 15 m depth. We attempted to address the potential bias associated with this by removing depth as a predictor, and also limiting the analysis to 30 m depth in the sensitivity analysis. There were no significant changes in the predictive performance of the model. However, harvest of sea cucumbers only occurs at depths that are accessible to SCUBA divers (< 30 m), so the potential bias in the survey data may not be a large issue. It may be worth exploring in further analysis though. Additionally, there may be sampling and positional uncertainty associated with the biological data. This includes the possibility that *P. californicus* may not have been seen on a surveyed transect at the time of surveying, but they may be present at another time of year which would impact the habitat suitability and density predictions.

Threshold selection is another large source of uncertainty when developing habitat suitability models. Most methods for selecting a threshold to differentiate between areas where a species is predicted to be present, and those where it is predicted to be absent, rely on statistical methods rather than biology. Consequently, some important biological drivers may be ignored. Selecting an appropriate threshold is challenging, and ideally the effectiveness of different thresholds should be tested in the field. If groundtruthing is not possible, it is advisable to test a range of possible thresholds, or simply use the gradient provided in the analysis rather than creating a Boolean response (i.e., present or absent).

2.4.7. Conclusion

The analysis in Section 2 has presented a demonstration of the use of BRT models to predict the distribution and density of a low-mobility benthic invertebrate species, the sea cucumber *P. californicus*. The models produced using these methods can be used in multiple ways to facilitate the formation of FCANs. Firstly, they can be used on their own to provide scientists and managers with valuable information on the predicted distribution and abundance of a species of interest in areas that have not yet been fully surveyed. These data can help guide

future research into the distribution, density of the species, as well as the environmental drivers that may be responsible for those responses. If the models are sufficiently reliable, they can also be used to help inform management decisions. Secondly, they can be used as input layers into additional modelling to explore the effect different FCAN designs have on meeting conservation and management objectives. This use will be further described and demonstrated in Section 3.

3. SIMULATION TOOL

3.1. INTRODUCTION

In this section, we build a simulation model that can be used to explore the effects of Fishery Closure Area Network (FCAN) designs on the probabilities of meeting conservation and management targets. The simulation model and results are constructed and analyzed with a set of tools available to the scientific community and customized to meet the objectives of this paper. We refer to the simulation model as a 'simulator'. The simulator consists of four sub-models of habitat suitability, dispersal, meta-population dynamics and fisheries management. The sub-models are coupled through various link functions. The metapopulation dynamics model uses outputs from the habitat suitability model to define the spatial structure, carrying capacity, and initial abundance of discrete populations. The dispersal model specifies how these discrete populations are connected through transport of larvae in the pelagic zone until they settle and recruit as juveniles in distant populations. The fisheries model defines the locations where different types of fishing occur, and the number of individuals removed at each time step. Such complex spatially-explicit models are increasingly used to assess species status, prioritize research, evaluate threats and inform management decisions for a broad range of species in terrestrial and aquatic systems (Akçakaya et al. 2004; Naujokaitis-Lewis et al. 2009; Naujokaitis-Lewis et al. 2013; Pe'er et al. 2013).

A common practice for development, analysis and application of coupled habitat-based metapopulation dynamics models is to carry out a whole-model sensitivity analysis (Saltelli et al. 2006: Naujokaitis-Lewis et al. 2009; Pe'er et al. 2013). Whole-model sensitivity analyses allow developers and users to quantify the influences of uncertainties in parameter values and model structures on simulation results. By identifying influential model parameters and assumptions, sensitivity analyses can be used to prioritize research, identify potential management intervention points, and develop management strategies that are robust to those sources of uncertainty. We use a global sensitivity analysis to evaluate the relative importance of a parameter on model predictions averaged across the entire parameter space. Specifically, our simulator allows users to measure the relative influences of parameters associated with habitat suitability, dispersal, population dynamics, and fisheries management including the number, size, and location of Fishery Closure Area Networks. Due to time constraints, we limit our sensitivity analysis to a subset of these parameters (Table 3-5). All parameters and functions included in our sensitivity analyses were varied independently.

Conservation and fisheries management objectives may relate to maintenance of a species' abundance and distribution patterns, its ecological functions, or demographic, behavioural or genetic diversity. Our set of tools allows users to evaluate network design primarily in relation to a species abundance and distribution patterns. They also allow users to consider alternative network designs using conservation and fisheries management criteria, including the percentage of populations occupied, population-specific or metapopulation abundance, probability of extinction, percent decline in the population, and probability of falling below a limit reference point. In the context of sea cucumber fisheries management, one objective would be to prevent the abundance within PFM Subareas from declining by more than 50% compared to

unfished biomass, the current limit reference point (Hand et al. 2009). In this paper, we consider the influence of model parameters on the magnitude of population decline expected at the end of 20 years and 100 years of fishing, and the likelihood that subareas will fall below the limit reference point. We modified GRIP to give the simulations 20 years to equilibrate prior to imposing fisheries management. This prevents our results in the first few years of fisheries management from being driven by initial conditions (Pe'er et al. 2013). We could have reported results for any specified time horizon. However, we report results at 100 years as this time horizon is commonly used in species assessments (e.g. IUCN 2012). We also report results at 20 years as this corresponds roughly to one human generation and was of interest to sea cucumber fishery managers.

The first component of our simulator is the predicted habitat suitability model (Section 2); this static part of the model is used to define the spatial structure of sea cucumber habitat patches that are suitable for survival, growth and reproduction in the study area (i.e. suitable habitat). In our simulation tool, patches of suitable habitat are assumed to support spatially-structured populations, thus the terms patch and population are treated synonymously (*sensu* Akçakaya and Root 2002). The second component of the simulator, the metapopulation dynamics model, simulates population-specific demography; spatially-explicit predictions of adult density (predicted density model from Section 2) are used to initialize population-specific abundances and carrying capacities. The third component, the dispersal model, is used as a basis for simulating the movement of larvae among populations. Thus metapopulation in this context is defined as a set of spatially-structured populations linked by dispersal. The final component of the simulator is the fishery management model. It simulates the effects of commercial, recreational, and First Nation fisheries on the demography of populations.

To evaluate the performance of alternative FCAN designs, we begin by identifying conservation and fishery management objectives. These objectives serve as performance criteria against which we compare the effectiveness of various FCAN designs. In this paper, we evaluate FCAN design in terms of its ability to prevent abundance within subareas from falling below the limit reference point (50% of unfished biomass). This performance criterion reflects the fact that commercial sea cucumber fisheries are assessed and managed at the scale of Pacific Fishery Management Subareas (described in more detail below). However, our simulator and set of tools allow users to evaluate alternative FCAN designs using conservation and fisheries management criteria, including the percentage of populations occupied, population-specific or metapopulation abundance, probability of extinction, percent decline in the population, and probability of falling below a limit reference point.

We develop a baseline scenario that represents the best available data, knowledge, and understanding about *P. californicus* distribution, population dynamics and dispersal, as well as the actual dynamics of fisheries in PFMA 12. We then carry out a whole-model sensitivity analysis (as in Curtis and Naujokaitis-Lewis 2008; Naujokaitis-Lewis et al. 2013) by randomly varying habitat, dispersal, and population parameters as well as commercial and other (e.g., recreational and First Nation) fishery management scenarios, and alternative FCAN network design scenarios in order to quantify the relative influences of all input parameters on model predictions. Model predictions generated during the sensitivity analyses are then used to investigate relationships between FCAN design (namely size, number, configuration, and connectivity of the sites that make up the network) and the probability of meeting conservation and fishery management objectives. Depending on the form and strength of these relationships following analysis of simulation results, model predictions can be used to identify optimal FCAN designs for meeting management objectives, and to develop simple rules of thumb for informing decisions on FCAN design in management areas with fewer data. The following section describes: the tools used to build the simulator, the structure of each of the four model sub-

components and how they are linked, the methods used to carry out the sensitivity analyses, and the analysis of model output.

3.2. METHODS

3.2.1. Software tools

We used a combination of RAMAS GIS software (Akcakaya and Root 2002) and R code to build a baseline metapopulation dynamics simulation model and carry out a comprehensive sensitivity analysis of the baseline model. RAMAS GIS is software that allows users to build single-species models of metapopulation dynamics that are spatially-explicit and linked to models of dispersal, harvest, supplementation, or other functions that govern population dynamics (e.g. disease transmission). It is one of the most widely used commercial software packages for assessing species status, performing population viability analyses, and assessing alternative management actions for species at risk (Naujokaitis-Lewis et al. 2009). The software has been applied to the analyses of fisheries management of Pacific herring and Atlantic herring (Akçakay et al. 2004), and in calculations of recovery targets for threatened and endangered freshwater fishes in Canada (Velez-Espino and Koops 2012). One of the limitations of this software, however, is the lack of functions for carrying out comprehensive sensitivity analyses of baseline models.

To compare the relative performance of alternative FCANs – given a high degree of uncertainty in habitat suitability, dispersal, population dynamics and fisheries management implementation – we used GRIP 1 (Generation of Random Input Parameters), a freely available open source program that facilitates computationally efficient and comprehensive analysis of the sensitivity of model predictions to changes in input parameters (Curtis and Naujokaitis-Lewis 2008). The program must be used with a baseline model developed with RAMAS software. It works by reading in the baseline model, randomly varying the values of input parameters by drawing on distributions specified in the code, producing batch files to run a specified number of scenarios and collating simulation results of interest into a comma delimited (CSV) file for further statistical analysis (e.g. boosted regression analysis, random forest analysis, Naujokaitis-Lewis et al. 2013). The program is written in R (RCDT 2011), an open source statistical programming language. GRIP 1 code is well annotated so that it can be easily modified to address different questions in sensitivity analyses or to incorporate functions or parameters that are specific to populations, species or areas. GRIP 1 has been customized in other studies to compare the performance of alternative minimum size limits for endangered marine fish managed by CITES (Curtis & Vincent 2008), to predict risks associated with climate change and range distributions for threatened birds (Naujokaitis-Lewis et al. 2013), to explore the effects of poaching on abalone population dynamics (Abbey Camaclang, University of Queensland, Queensland, Australia, unpublished data) and to provide advice on the amount and configuration of critical habitat needed to meet specified recovery goals (Janelle Curtis, Fisheries and Oceans Canada, Nanaimo, BC, unpublished data).

3.2.2. Study area

The study area used for the simulation tool covers most of PFMA 12 (Figure 3-1). The only exceptions are the elimination of approximately half of PFM Subarea 1 and all of Subarea 25. These were removed to match the extent of an ocean circulation model that exists for this area.

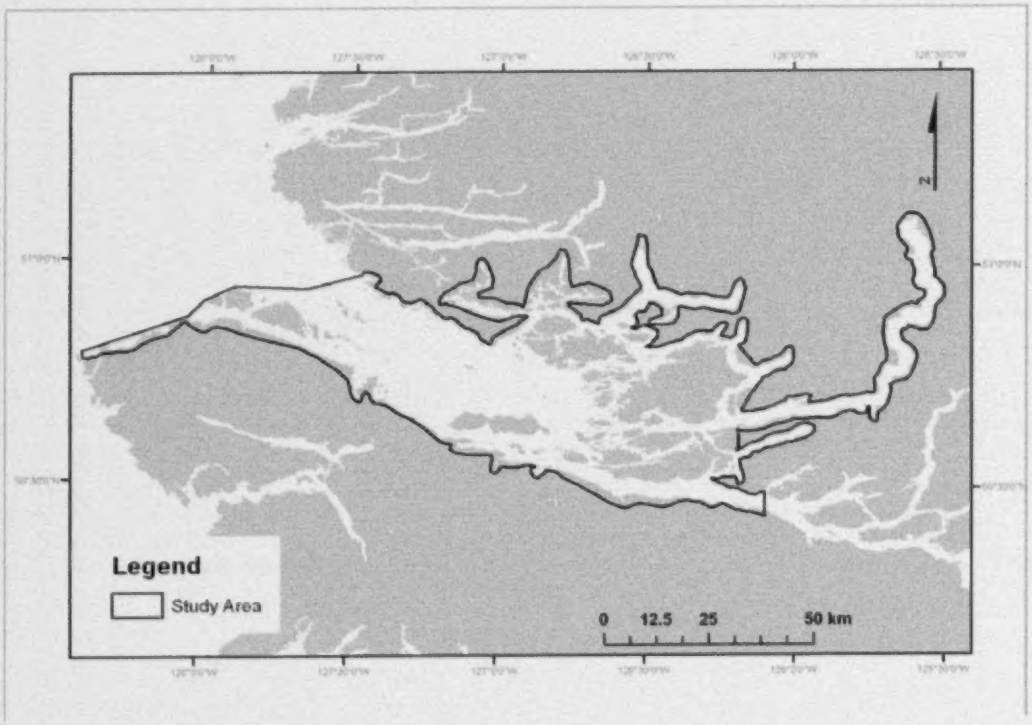

Figure 3-1. The study area for the simulation tool. The area covers most of Pacific Fisheries Management Area (PFMA) 12, except for approximately half of PFM Subarea 1 and all of PFM Subarea 25 (both in the southeast corner of the study area.)

3.2.3. Simulator sub-component descriptions and parameterization

In the following section we describe the four sub-components of the simulator and how they were parameterized. The sub-components include:

1. a habitat suitability model;
2. a metapopulation dynamics model;
3. a dispersal model; and
4. a fisheries management model.

For each model a description is provided for the parameters used in both the baseline scenario (our best approximation of reality) and a range of parameter values explored in sensitivity analyses. Whole-model sensitivity analysis is considered a best practice for the development, analysis and application of coupled habitat-based metapopulation dynamics models (Saltelli et al. 2006: Naujokaitis-Lewis et al. 2009; Pe'er et al. 2013). Whole-model sensitivity analyses allow developers and users to quantify the influences of uncertainties in parameter values and model structures on simulation results. By identifying influential model parameters and assumptions, sensitivity analyses can be used to prioritize research, identify potential management intervention points, and develop management strategies that are robust to those sources of uncertainty. Our tool allows users to measure the relative influences of parameters associated with habitat suitability, dispersal, population dynamics, and fisheries management including the number, size, and location of Fishery Closure areas. Due to time constraints, we

limit our sensitivity analysis to a subset of these parameters (Table 3-6). All parameters and functions included in our sensitivity analyses were varied randomly and independently.

3.2.3.1. Spatial structure of discrete populations

In this simulator– as is often assumed in habitat-based, spatially-explicit metapopulation models (Akcakaya and Root 2002) – patches of suitable habitat are assumed to support spatially structured populations of sea cucumbers that are linked to each other via dispersal. Thus discrete patches of suitable habitat are treated as subpopulations within a metapopulation. However the true spatial structure of discrete sea cucumber populations is not known and may not correspond to the spatial structure of suitable habitat. Also, sea cucumbers may not meet the criteria for a strict definition of metapopulation, whereby dynamics are driven by local extinction and recolonization processes. Nevertheless, ours is a convenient approach for simulating the dynamics of spatially structured groups of individuals, as well as the movements of individuals among those groups, while maintaining tractable computations. We defined patches of suitable habitat on the basis of a habitat suitability threshold, depth, and a neighbourhood distance. Habitat suitability thresholds are used to distinguish habitat of sufficient quality to support survival, growth and reproduction. The analyses used to identify the amount and distribution of suitable habitat are described in Section 2. In our baseline scenario, the habitat suitability threshold was selected as 0.75 (see Section 2 for a justification for using 0.75). Although *P. californicus* is recorded to depths of 256 m in BC (N. Duprey, personal observation), areas of suitable habitat in our simulations were restricted to depths equal to or shallower than 30 m. The occurrence data used to build the habitat suitability model is from surveys occurring in water equal two or shallower than 15 m. It seems biologically reasonable to extrapolate those data into slightly deeper water that are still within diveable depths (30 m) where they are known to regularly exist and reproduce (N. Duprey, personal communication). However, there are no data on the presence, distribution and reproductive capability of *P. californicus* in water deeper than 30 m. Therefore the authors felt it was more precautionary to presume that area below 30 m were not suitable for the survival, growth and reproduction of populations of *P. californicus*. Additionally few fishers harvest sea cucumbers below this depth, and so any sea cucumbers below 30 m are not accessible to the fishery, nor are they considered in stock assessments. The neighbourhood distance is used to combine discrete patches of closely-spaced suitable habitat into spatially-structured populations. In our case, we arbitrarily set the neighbourhood distance to 850 m as this was the smallest neighbourhood distance we could use while maintaining the computations required for tractable simulation. RAMAS GIS default settings require that the maximum number of patches be less than 500 populations. By setting the neighbourhood distance to 850 m, we could reduce the number of spatially discrete populations in our simulations to 370. While assuming a neighbourhood distance of 850 m makes the computations more tractable, this distance may be larger than the typical foraging or home range distance of most sedentary invertebrates including sea cucumbers.

RAMAS has a built-in function to define habitat patches on the basis of neighbourhood distances. However, it does not allow for the inclusion of impassable barriers, such as land. Habitat patches were therefore calculated using several tools in ArcMap 10.0 (ESRI 2011). First, the Cost Distance tool in the Spatial Analyst extension was used to calculate the cumulative distance, measured from center point to center point, from each patch of suitable habitat (two or more adjacent cells of suitable habitat) to every other raster cell in the study area. To the greatest extent possible, land was included as a barrier to more accurately represent connectedness between cells of suitable habitat. For example, the distance between two nearby cells of suitable habitat that were separated by a peninsula would be measured around the peninsula rather than across it. The Reclassify tool was then used to select only those cells that fell within the defined neighbourhood distance of each cell of suitable habitat

(Figure 3-2A). If the buffer around a cell of suitable habitat did not touch another buffer, it was considered a unique habitat patch (Figure 3-2B, left). However, if the buffer of one or more cells of suitable habitat overlapped or were touching the buffers of other cells of suitable habitat, they were all joined into a single habitat patch (Figure 3-2B, right). The reclassified raster was then converted into discrete polygons representing each habitat patch. Management scenarios in the population dynamics model operate on a PFM Subarea level; in order to simulate those cases when different fisheries management actions were applied to different parts of a population straddling multiple PFM Subareas patches overlapping PFM Subarea boundaries were further divided along boundary lines (Figure 3-2C and D). Algorithms used in RAMAS require habitat patches to be separated by at least one cell, so the habitat suitability of cells that fell along PFM Subarea boundaries were set to zero (Figure 3-2E). This resulted in a very small proportion of habitat area (< 5%) being removed. In total 370 discrete habitat patches were identified using a habitat suitability threshold of 0.75 and a neighbourhood distance of 850 m (Figure 3-3). To circumvent the "find patches" routine in RAMAS GIS, this map of discrete patches was imported into the RAMAS GIS Spatial Module as an ASCII file where suitable and unsuitable habitat were set to 1 and 0, respectively, and the neighbourhood distance was set to 1.

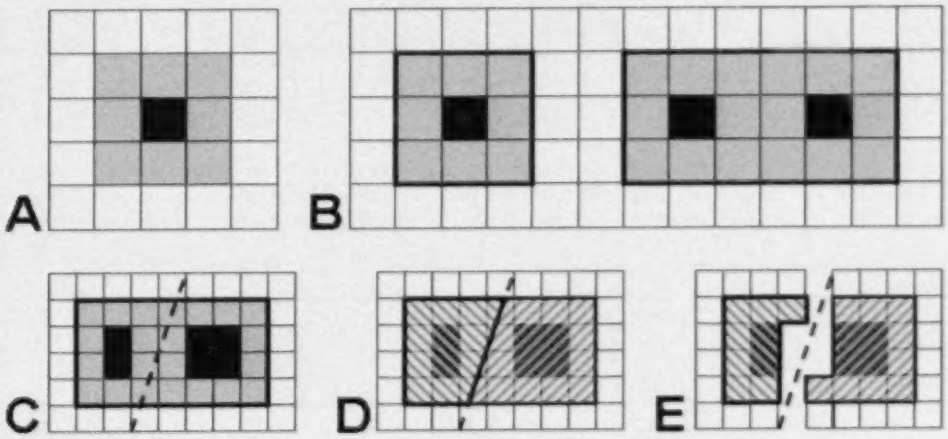

Figure 3-2. Schematics of how habitat patches were formed. Cells of suitable habitat are represented in black, while the buffer, or neighbourhood distance, is grey and white cells are cells of neither suitable habitat nor within the buffer distance from a cell of suitable habitat. A) A single 300x300 m cell of suitable habitat surrounded by a buffer with a neighbourhood distance of 850 m. B) Two habitat patches, outlined in black. The first (on the left) is a single cell of suitable habitat and its buffer, while the second (on the right) shows two cells of suitable habitat whose buffers are directly adjacent to one another. They are therefore joined into a single patch of habitat. C) A single habitat patch that is crossed by a PFM Subarea boundary (dotted line). D) Two separate habitat patches (indicated by diagonal lines) after being split by a PFM Subarea boundary. E) The two resulting separate habitat patches after cells along the PFMA Subarea boundary have been deleted.

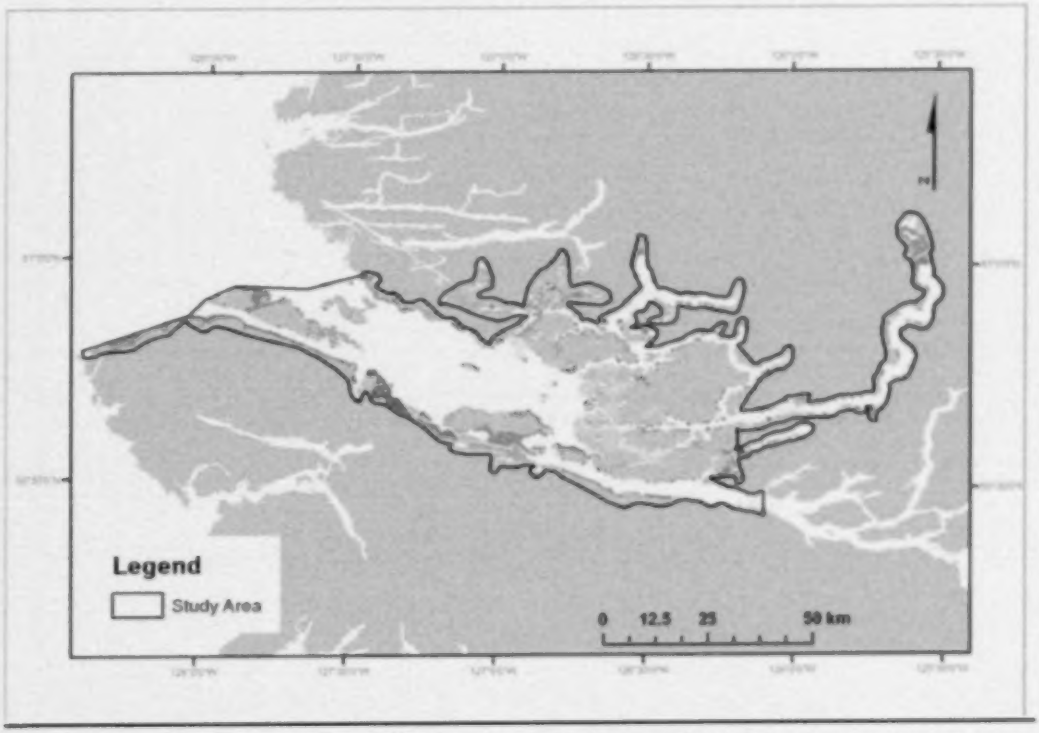

Figure 3-3. Map of the 370 populations of Parastichopus californicus identified using a habitat suitability threshold of 0.75 and a neighbourhood distance of 850 m, excluding suitable habitat deeper than 30 m. Each population is represented by a different colour.

The habitat suitability threshold and neighbourhood distance for *P. californicus* in PFMA 12 are important parameters in our simulator as they influence the number, configuration and size of each habitat patch, which informs the overall metapopulation structure. We used the maximum sum of sensitivity-plus-specificity to select a habitat suitability threshold that effectively balances sensitivity and specificity (Jiménez-Valverde and Lobo 2007), which in our baseline model was 0.75. We then used the smallest neighbourhood distance that produced fewer than 500 populations in combination with the baseline habitat suitability threshold. However, the true values for the habitat suitability threshold and the neighbourhood distance are unknown.

GRIP 1 was originally designed to investigate the effects of uncertainties associated with landscapes and the distribution of suitable habitat by varying the habitat suitability threshold and neighbourhood distances in a sensitivity analysis. In our analysis, we varied the habitat suitability maps directly to address these sources of uncertainty because of computational challenges associated with recalculating the matrix of distances among all pairs of populations (i.e. pairwise population distances) for each replicate scenario. For similar reasons our version of GRIP does not vary the number of populations in the landscape. These are acceptable changes to the code because in our case we are primarily interested in the influence of reserve design as opposed to uncertainty in the population structure. Instead of varying the location of suitable habitat automatically in our sensitivity analysis, we vary the location, size, and number of populations that are part of an FCAN in each scenario. In order to facilitate sensitivity analyses with alternative habitat structures produced manually, we added code to allow us to vary and build a baseline metapopulation dynamics model (i.e. *.mp file) automatically by

reading in CSV and ASCII files that define alternative habitat suitability maps and corresponding matrices of pairwise distances.

To account for these sources of uncertainty, a total of 13 metapopulation structures (one of which was the baseline, described above) were derived from combinations of 4 habitat suitability thresholds (0.7, 0.75, 0.8, and 0.9) and 4 neighbourhood distances (600 m, 850 m, 1450 m, and 1700 m; (Table 3-1). Some combinations (neighbourhood distance of 600 m with the thresholds of 0.7, 0.75 and 0.8) were not possible as they resulted in more populations than RAMAS could handle. The intention was to use these 13 metapopulation structures in our whole –model sensitivity analyses to explore the influence of uncertainties associated with the baseline habitat suitability map on our simulation results. The simulation tool is designed to allow users to quantify the uncertainties associated with the amount and location of suitable habitat and their influences on model results. However, only the baseline metapopulation structure is explored in this paper.

Table 3-1. Summary of the sensitivity, specificity, number of populations, initial abundance and area (suitable habitat and neighbourhood distance buffer) for all alternative habitat suitability scenarios prepared. The baseline scenario 0.75 (bold) is the only one used in the presented simulation results. ND, is the neighbourhood distance.

Threshold	ND	Sensitivity	Specificity	Number of populations	Initial abundance	Area (km^2)
0.70	850 m	0.940	0.624	428	116,293,312	1017
	1450 m	-	-	294	-	1328
	1700 m	-	-	272	-	1409
0.75	**850 m**	**0.896**	**0.785**	**370**	**56,388,900**	**975**
	1450 m	-	-	305	-	1294
	1700 m	-	-	279	-	1377
0.80	850 m	0.822	0.839	418	101,206,215	886
	1450 m	-	-	303	-	1207
	1700 m	-	-	277	-	1292
0.90	600 m	0.263	0.989	384	48,585,396	408
	850 m	-	-	316	-	533
	1450 m	-	-	232	-	798
	1700 m	-	-	221	-	868

3.2.3.2. Metapopulation Dynamics Model

The core of the demographic model is a stage-based matrix upon which several functions operate to simulate population processes including density-dependent population growth and

density-independent dispersal. A stage-based matrix model keeps tracks of the number of individuals in each life history stage included in the model and their contributions to other life history stages through growth, reproduction or other processes. Given the lack of population-specific estimates of vital rates (i.e. stage-specific survival and fecundities), this same core matrix model is assumed for all populations in our simulations. Few data are available to estimate the life history parameters for *P. californicus*. We therefore constructed our demographic model using what information is currently available for this species (e.g. Cameron and Fankboner 1986, 1989; Fankboner and Cameron 1988; Hannah et al. 2012) and by drawing on data from previous simulation studies (e.g. Humble 2005; Humble et al. 2008; Hand et al. 2009; Hajas et al. 2011), unpublished data, expert judgment, and published information on related species to provide a baseline and a range of values for unknown or highly uncertain parameters. In the following sections, we describe the life stages considered in the population dynamics model, the methods and data used to parameterize fecundity and survival rates of each stage, and then the functions that govern metapopulation dynamics in our simulations.

Table 3-2: Lefkovich matrix of stage-specific fecundities and transition probabilities (S) for mixed sexes, including baseline values. The fecundity of adult females is represented by f_a, and is multiplied by 0.5 to account for an equal sex ratio. g_{12}, g_{23} and g_{34} are the probabilities of survival from age 1 to 2, age 2 to 3 and 3 to 4, respectively. g_{11} and g_{44} represent the probabilities of surviving and remaining in the juvenile stage for an additional year or surviving and maturing to the adult stage, respectively. g_{aa} is the survival probability of adults. Transition rates are applied to stage-specific abundances at each time step, which in our model, corresponds to a year. j_1 are animals almost 2 years old; j_2 are animals almost 3 years old; j_3 are animals almost 4 years old; j_{4+} are animals greater than 4 years old.

	j_1	j_2	j_3	j_{4+}	**Adults**
j_1	0	0	0	0	$0.5*f_a$
j_2	g_{12} 0.20	0	0	0	0
j_3	0	g_{23} 0.20	0	0	0
j_{4+}	0	0	g_{34} 0.69	g_{44} 0.5	0
Adults	0	0	0	g_{aa} 0.19	g_{aa} 0.69

A Lefkovich matrix (Caswell 1989) of stage-specific fecundities and transition probabilities (Table 3-2) was used as the basis for simulating population demography and growth because of the challenges associated with ageing sea cucumbers and the lack of age-specific data for *P. californicus* (Boutillier et al. 1998; Hand et al. 2009). The key assumption of stage-based matrices is that all individuals within a stage experience the same survival, growth, and fecundity rates (Crouse et al. 1987). In a stage matrix, the value in the i^{th} row of the j^{th} column represents the proportion of individuals in the j^{th} stage that transition to the i^{th} stage (Akçakaya and Root 2005). GRIP 1 includes simple code for reading in survival and fecundity rates for age-

based matrices. Because ours is a stage-based matrix, we customized the code to read in and record all the transition probabilities, as described below.

We group individuals into five stages based on their development, habitat use, size, and vulnerability to fishing.

Adult *P. californicus* are broadcast spawners (Phillips and Boutilier 1998). Larvae survive, disperse and grow in the pelagic zone until they settle on benthic substrate as juveniles. The larval period is estimated to range from 51 to 125 days (Strathmann 1978; Cameron and Fankboner 1989). In our baseline scenario we assume that larvae drift pelagically until they settle onto suitable benthic habitat as juveniles where they experience high mortality associated with predation during their first year. We implicitly simulate larvae that are born, survive and grow as described below, but do not reproduce. Larvae are assumed to be highly vulnerable to predators and exhibit cryptic behaviours both in the pelagic zone and as they settle onto benthic substrata. Larvae and young juveniles are rarely observed during surveys (Cameron and Fankboner 1989; Hand et al. 2009).

The first two stages in our model represent juveniles that are in their second (j_2, just about to turn 2 years old) and third (j_3, just about to turn 3 years old) years that survive and grow, but do not reproduce and are not harvested. All surviving individuals spend one year in each stage. The residence time of juveniles in each of these stages is one year.

The third stage in our matrix represents juveniles that are in their fourth year (j_4, just about to turn 4 years old) that survive and grow, but do not reproduce and are not harvested. In their fourth year, they are assumed to be large enough to evade predation by sea stars (Cameron and Fankboner 1989) but are still not reproductively mature. The residence time of juveniles in this stage is one year.

The fourth stage in our matrix, j_{5+}, represents juveniles that are at least four years old. Age at maturity is unknown in this species, but juveniles are estimated to mature after 5 years of age (Fankboner & Cameron 1985; Humble 2005). Of those individuals that survive one year in this stage, a proportion remains immature while the remainder mature into adults. The average residence time in this stage is two years. Juveniles in this stage are not harvested in our simulations because recruitment to the fishery is assumed to begin at 5-8 years of age (Fankboner & Cameron 1988; N. Duprey, Fisheries and Oceans Canada, Nanaimo, BC, unpublished data). This is because fishers tend to select larger, and therefore older, individuals.

The fifth stage represents adults that survive, grow, and reproduce and are subject to commercial, recreational and First Nation fishing mortality. The maximum age of *P. californicus* is not known, but in our model is defined by the transition probabilities; the proportion of each cohort that remains in the adult stage diminishes at a rate of 1- g_{ad} until all individuals in that cohort have died. In our baseline scenario, individuals that survive to the adult stage survive on average an additional 3.23 years and approximately 1% survive for 12 years as adults. In our sensitivity analysis, we explore a range of adult survival rates whereby average residence times ranged from 2.13 to 7.14 years, and approximately 1% of individuals spend 7 – 30 years as adults before they die.

The top row of the stage matrix represents stage-specific fecundities while the remaining cells represent the transition probabilities (Table 3-2). In our matrix, only adults produce juveniles, j_1, that are just about to turn one year old at the end of each time step. The matrix assumes an equal sex ratio (Cameron and Fankboner 1986), simulates both sexes together (i.e. mixed sexes), and assumes, for simplicity, that all individuals are born in a single pulse (i.e. birth pulse).

Fecundity of adults (fa)

In our model, we define fecundity as the number of viable larvae produced by mature females multiplied by larval survival rate at each time step (i.e. recruits per adult per time step). In the case of broadcast spawners, like *P. californicus*, the effective number of larvae produced per adult female is a function of the proportion of mature females spawning at each time step, the number of viable eggs produced, the fertilization efficiency, and the proportion of larvae that disperse to and settle in suitable habitat. None of these parameter values are known for *P. californicus*, therefore we use a two-pronged approach to define baseline fecundity and the ranges explored in a sensitivity analysis.

In our first approach we begin by assuming that at $t = 0$, the metapopulation of sea cucumbers in PFMA 12 is at or near an equilibrium population size, or the carrying capacity, K. In the absence of density-dependent processes or other density-independent factors that might influence population abundance trends, we assume that lambda (the dominant eigenvalue) in our matrix model is 1. To achieve a lambda = 1 with the transition probabilities assumed for our baseline model (described below), fecundity must be 30 recruits per adult per time step (λ = 1.00138). However, because fecundity is an uncertain parameter, we crosscheck our estimated baseline fecundity value, and determine a plausible range of values to use in the sensitivity analysis, by calculating it a second way. We synthesized available information on the proportion of mature females spawning at each time step, number of viable eggs produced, the fertilization efficiency, and the proportion of larvae that disperse to and settle in suitable habitat. For each unknown value we drew on expert knowledge, simulation results, or published estimates from related species to define a range of plausible values, and used those ranges to calculate a plausible minimum and maximum value for fecundity.

The proportion of females breeding each year is unknown for *P. californicus*. In our baseline simulation, we assumed the proportion of females spawning at each time step to be 0.9 to account for variability in the size and age at physiological and behavioural maturity, and the sublethal effects of a variety of stressors that may affect individuals, including diseases, injuries, and food limitations.

There were no estimates of the annual reproductive output of *P. californicus* available in the literature and no unpublished estimates to the best of our knowledge. Therefore we estimated the number of oocytes produced by adults with a statistical model fit to published estimates of the number of oocytes per gram of body wall (in 1,000s), y, and adult body wall weight, x, available for nine tropical sea cucumber species (Conand 1993, Figure 3-4). Allometric approaches to estimate life history parameters are widely used to address gaps in biological information when developing population dynamics models. The estimates were obtained from Figure 6 in Conand (1993) using DataThief (B. Tummers, DataThief III, 2006). The equation of the fitted line (adjusted r^2 = 0.76, p = 0.0014) was:

$$y = 97.46 * e^{0.0025x}$$

Surveys of *P. californicus* included random transects where 25-30 animals were collected then split longitudinally and weighed without gut or coelomic content (Hand et al. 2009, Duprey et al. 2011). The mean and standard deviation of body wall weight (i.e. split and drained weight) of *P. californicus* collected from 2000-2010 in PFMA 12 was 304.17 g ±112.18 g (n=1469). Based on this allometric relationship, the mean number of oocytes per gram of body wall for large adult *P. californicus* was predicted to be 48,343 (± SD of 16,260), and the total expected annual oocyte production (± SD) of a large adult female was calculated as 14,704,490 (± 7,339,639), taking into consideration the SD in weight and uncertainty in the predicted y.

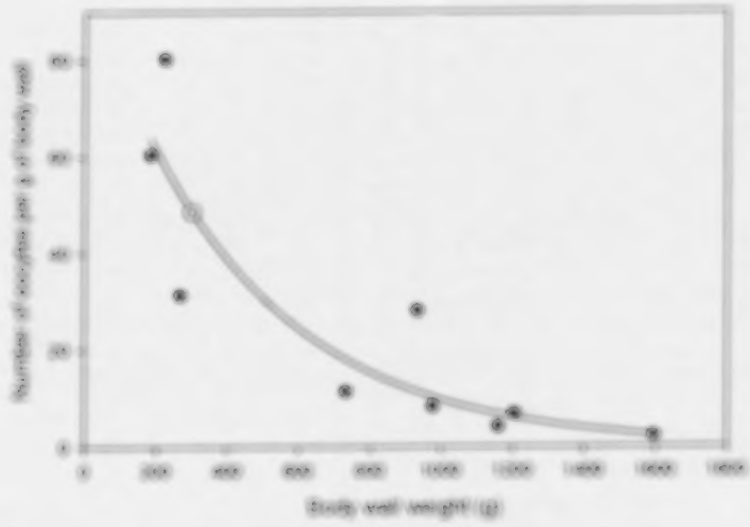

Figure 3-4. Model fitted to estimates of the number of oocytes per gram of body wall as a function of body wall weight (g) for 9 species of sea cucumber (solid circles). The predicted number of oocytes per gram of body weight for adult P. californicus is represented by the open circle. The number of oocytes per g of body wall is in 1,000s. Estimates were extracted from Figure 6 in Conand (1993) with DataThief (Tummers 2006).

Egg viability is unknown in *P. californicus* and is probably difficult to estimate using histological examinations of oocytes. One laboratory study of *Cucumaria frondosa* larval rearing (Hamel and Mercier 1996) reported that approximately 45% of eggs were lost before or during fertilization, which we assumed in our calculations of fecundity. These losses were attributed in part to nonviable eggs, or eggs that were fertilized by multiple spermatozoa.

Because *P. californicus* are synchronous broadcast spawners, fertilization rates may be influenced by release timing, spawner density, and environmental factors such as current speed (Pennington 1985). Fertilization rates, however, are unknown in this species, but have been reported to range from 0.69 to 0.9 in laboratory studies of *C. frondosa* (Hamel and Mercier 1996) and *Australostichopus mollis* (Morgan 2000), respectively. These fertilization rates are much higher than observed *in situ* where up to 40% of echinoderm eggs were fertilized by males within 2 m of release point (Pennington 1985). In our calculations, we assumed that the fertilization rates can range from 1% to 40%.

Following spawning, embryos/larvae are distributed to surrounding patches of habitat via currents and tides. The behaviour of developing larvae while dispersing is not known, and was not accounted for in our simulations. The literature indicates that *P. californicus* larvae are assumed to drift in pelagic waters for 51-125 days (Strathmann 1978; Cameron and Fankboner 1989). In our simulation 90 days, the approximate mid point of the estimated range, was selected for the baseline scenario. The fate of larvae is generally governed by their behaviour, species interactions, ocean circulation patterns, tidal influences and other characteristics of the water therefore it is difficult to predict the location that larvae will disperse to and settle on and the number that will survive to settlement. In the absence of information about ocean circulation patterns and larval dispersal/survival for *P. californicus*, we assume that the proportion of larvae

that successfully disperse to and settle on suitable habitat is the same as the proportion of suitable habitat available in less than 30 m depth within the study area (~10%).

Taking into consideration the proportion of mature females spawning at each time step, number of viable oocytes produced, the fertilization efficiency, and the proportion of larvae that disperse to and settle in suitable habitat, our baseline estimate of the number of larvae produced is 180,409. The lower and upper quartiles of plausible values were 3,725 and 520,344, respectively. The degree to which egg production varies interannually is unknown and was not reported for any species in our literature review.

Allee effects were ignored in our simulations because of the lack of information available on fertilization rates at low population abundance, and because our predicted initial population sizes are based on surveys of areas where commercial fishing had not taken place in recent years (i.e. metapopulation abundance is at or close to equilibrium).

In order to calculate an estimate of fecundity, we need to multiply the number of larvae produced by their survival rate. Larval survival rate, S_L, is the annual survival rate of larvae which settle as juveniles during their first year. Survival rates of early life history stages are generally unknown in marine invertebrates, and sea cucumbers are no exception. However, some data are available on the survival rates of sea cucumber larvae reared in experimental aquaria for short periods of time (e.g. a few weeks to several months, Table 3-3). We use published estimates of daily survival rate from a variety of sea cucumber species to estimate the survival rate of larvae until they settle at 30 days, assuming that larval survival is constant until they settle onto benthic substrates. The mean (± SD) of these estimates is 3.1% (±3.15%), but it may be far less in the wild due to predation, food limitations and unfavourable ocean conditions. Once settled, we arbitrarily assume that 1/3rd survive to the end of their first year (i.e. $S_A = 0.333^{1/3}$).

Table 3-3: Published estimates of sea cucumber larval survival rate.

Source	Species	Survival rate (%)	Time (days)	Daily survival rate
Ashe & Wulff (2005), average of optimal treatments	*Holothuria spurilla*	84.3	10	0.9881
Quinzio et al. (2001)	*Athyonidium chilense*	1.24	240	0.9732
Krauss (2011), average of feeding trials	*Holothuria scabra*	48.2	10	0.9077
Li et al. (2011), average of optimal treatments	*Apostichopus japonicus*	80.3	9	0.9879
Mercier & Hamel (1999)	*Cucumaria frondosa*	10	17	0.8643
Morgan (2000), average of treatments	*Australostichopus mollis*	40	20	0.9554

By multiplying the plausible ranges of the average number of larvae produced per female at each time step by plausible estimates of larval survival, the 25th percentile of fecundity values was calculated as 3.2 recruits per adult per time step, which would result in a declining

population in a deterministic model with $\lambda = 0.83$. By contrast the 75th percentile was 44.8 recruits per adult per time step, which corresponds to an increasing population in a deterministic model with $\lambda = 1.053$. Thus the fecundity value we use as our baseline, 30 recruits per adult per time step, falls within the range of plausible values determined on the basis of expert knowledge, simulations, and studies based on related species.

Juvenile survival rates (g_{12}, g_{23}, g_{34}, g_{44}, g_{45})

The survival rate of benthic juveniles is not known, although experimental studies of the survival of juvenile sandfish, *Holothuria scabra*, released onto soft substrata near mangrove, seagrass and coral flat habitats suggest that they are highly vulnerable to predation at this stage (Dance et al. 2003). Cameron and Fankboner (1989) reported that predation by *S. dawsoni* was more prevalent on small size classes compared to larger size classes in aquarium experiments. Thus we assumed in our baseline that j_1 and j_2 share a relatively higher vulnerability to predation by other echinoderms than older, larger juveniles. Specifically, in our baseline model, we assume that the annual survival rates of j_1 and j_2 are 0.2 and we varied these survival probabilities from 0.15 to 0.25 in our sensitivity analysis. However, j_2 individuals may survive at rates closer to 0.3-0.4 if they are larger than 3-4 cm in length (Matt Slater, personal communication). In their fourth year, juveniles are assumed to be large enough to evade predation by most predators, including other echinoderms, and therefore are predicted to have the same survival rate as adults (0.69, see below). In their 5th year, juveniles are assumed to have the same survival rate as adults, however, a proportion of these juveniles transition to the adult stage. At each time step, 0.31 are assumed to die of natural causes, 0.5 survive and remain in this stage, and 0.19 mature and transition to the adult stage. Future simulations could explore the influence of survival rates of juvenile sea cucumbers which may be higher than assumed in this paper (e.g. varying j_2 from 0.15 to 0.4)

Adult survival rate (g_{44})

Most published estimates of adult natural mortality rate, M, are derived from stock assessments or simulation models (Table 3-4) whereby annual survival rate is calculated as:

$$S = e^{-M}$$

No estimates of survival or mortality rate were available for *P. californicus*. Therefore we calculated annual survival rate based on the value of M assumed by Humble (2005) and Humble et al. (2008) in analyses of rotational harvest rates for this species in BC, where g_{44} = 0.69 (Table 3-4). In our sensitivity analyses, we varied g_{44} from approximately 0.55 to 0.85, which includes most estimates of adult survival available for related species (Table 3-4). This range corresponds roughly to maximum ages of 13 and 30 years, respectively, in our model. The degree to which larval, juvenile and adult transition probabilities vary over time is unknown and was not reported for any species in our literature review. We assumed transition rates varied lognormally with a coefficient of variation (CV) of 20%.

Table 3-4: Estimates of the instantaneous natural mortality, M (or annual survival rate, S) of adult sea cucumbers, converted to annual survival rate.

Source	Species	*M*	*S* (year^{-1})	Comments
Jensen (1996,1997) as cited in Herrero Pérezrul & Chávez (2005)	*Parastichopus parvimensis*	1.50	0.223	Natural mortality, where S = 100*e^-M
Pauly (1980) and Rikhter & Efanov (1976), as cited in Chavez et al. (2011)	*Parastichopus parvimensis*	0.83	0.436	Natural mortality, where S = 100*e^-M
Hoenig (1983) as cited in Chavez et al. (2011)	*Parastichopus parvimensis*	0.85	0.427	Natural mortality, where S = 100*e^-M
Jensen (1996, 1997) as cited in Chavez et al. (2011)	*Parastichopus parvimensis*	0.90	0.406	Natural mortality, where S = 100*e^-M
Hearn et al. (2005)	*Isostichopus fuscus*	0.174	0.840	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Actinopyga echinites*	0.80	0.449	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Actinopyga miliaris*	0.50	0.606	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Bohadschia marmorata*	0.18	0.835	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Bohadschia sp. "lines"*	1.12	0.326	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Bohadschia vitiensis*	0.70	0.496	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Holothuria atra*	0.38	0.683	predicted from stock assessment

Source	Species	*M*	*S* (year^{-1})	Comments
Dissanayake and Stefansson (2012)	*Holothuria fuscogilva*	0.54	0.582	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Holothuria scabra*	0.47	0.625	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Holothuria spinifera*	0.21	0.810	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Stichopus chloronotus*	0.30	0.740	predicted from stock assessment
Dissanayake and Stefansson (2012)	*Thelenota anax*	0.17	0.843	predicted from stock assessment
Humble (2005) and Humble et al. (2008)	*Parastichopus californicus*	0.37	0.690	based on simulations, and maximum age of 14

Given the baseline fecundities and transition probabilities, the dominant eigenvalue of the matrix (i.e. λ, Caswell 1989) is 1.0018. Thus populations in our baseline scenario are predicted to grow at a negligible rate of 0.18% in the absence of any functions that operate on the matrix (e.g. density dependence, stochastic processes, exploitation). Below we describe two additional functions that influence population size and growth and how these functions were parameterized.

Initial abundance of adults

In our simulations we track the abundances of all five stages in each population at each time step. However, except when otherwise specified, abundance refers only to the abundance of adults. In the baseline scenario the initial abundance for each habitat patch was calculated by multiplying the area (in m^2) of all suitable habitat in each patch by the mean predicted density (in sea cucumbers/m^2) of all the cells of suitable habitat in the patch (see population density model predictions in Section 2). In our sensitivity analysis, population abundances were varied by drawing from normal distributions with a mean equal to the population's calculated carrying capacity and assuming a CV of 20% (Table 3-6).

For this study, we only report trends in abundance of adults because fishers tend to select larger individuals when fishing and juveniles are infrequently encountered and counted in fishery-independent surveys. Our carrying capacity values are therefore expressed in terms of the number of adults per population. Because initial abundances in RAMAS models must include all individuals from all modeled stages, we added some code to predict the initial abundances of juvenile stages based on adult abundances and assuming a stable stage distribution.

Density-Dependence

The effects of density-dependence on vital rates were simulated at each time step by calculating the expected rate of population growth, R_t, and adjusting the affected vital rates equally to achieve the predicted R_t (Akçakaya and Root 2002). The baseline model of density-dependence is a Beverton-Holt model, based on published population growth models available

for other sea cucumber species (Herrero Pérezrul and Chávez 2005; Chavez et al. 2011). The form of the Beverton-Holt function is:

$$R_t = R_{\max} * e^{\left(\frac{-\ln(R_{\max}) * N_t}{K}\right)}$$

And the form of the Ricker function is:

$$R_t = \frac{R_{\max} * K}{R_{\max} * N_t - N_t + K}$$

Where, in both equations, R_t is the expected population growth, R_{max} is the maximum number of recruits produced per adult female per time step, N_t is the population size of large adults at time t, and K is the carrying capacity of the population. The ceiling model predicts that population abundance will either grow according to λ, the dominant eigenvalue of the Lefkovich matrix, until it reaches K, or it will decline according to λ until it reaches zero (Akcakaya and Root 2002). In a global sensitivity analysis, one would typically vary the model of density dependence (e.g. Curtis and Vincent 2008) to account for uncertainty in the nature and strength of density-dependent population growth. Due to time constraints, we did not vary the model of density dependence and only used the Beverton-Holt model. However, our simulation tool has the capacity to consider a variety of models of density dependence in population growth, including a Ricker function, ceiling model, exponential growth, and any of these in combination with Allee effects. All three models are coded into the simulator tool and all three could be run with or without Allee effects in a global sensitivity analysis in the future.

Density-dependence is assumed to affect all populations in the same manner, and to affect the vital rates of all benthic individuals, specifically the survival rates of juveniles and adults, as well as fecundities. For our baseline simulation, we used an R_{max} of 1.27 which is the average of published estimates for *Isostichopus fuscus* (1.25, Herrero Pérezrul & Chávez 2005) and the warty sea cucumber, *Parastichopus parvimensis* (1.29, Chavez et al. 2011). The carrying capacity, K, for large adults in each population was assumed to be the same as initial abundance because these were based on estimates derived from unfished populations assumed to be at or close to equilibrium population size. However, in our sensitivity analysis, we varied K independently of initial abundance by drawing from the same distribution for each population (Table 3-6).

Stochasticity

Environmental conditions in ecosystems are rarely static, but rather change over a range of spatial and temporal scales. The Pacific decadal oscillation and El Nino are two examples of periodic changes in environmental conditions that influence the distribution and abundance of marine organisms in BC. In order to represent changes in environmental conditions that could influence the dynamics of sea cucumbers, we randomly varied the carrying capacity, K, at each time step by drawing from a normal distribution with a mean K and an estimated standard deviation. In our paper, the standard deviation in K was calculated based on abundance estimates obtained from a long-term monitoring study of unfished sites from 1997 to 2007 (Hand et al. 2009). These unfished areas were control sites in a study of the effects of fishing in experimental fishing areas (EFA). The data from the EFA control sites were obtained by monitoring the densities of *P. californicus* in four 10,000 m segments of shoreline using SCUBA. The density of each of the four areas was calculated within years and sites. For each site, the mean and standard deviation of density was calculated to obtain at estimate of the coefficient of variation (CV) in abundance across years. Then a mean (± SD) of CVs was calculated across the four sites as 0.18 (± 0.9). In our baseline scenario we assumed that the CV in K was 0.18

(Table 3-6). In our sensitivity analysis, the CV in K was randomly drawn from a normal distribution with mean = 0.18 and SD = 0.9 (Table 3-5).

In our analyses, we did not simulate or record any effects of local or regional catastrophes due to lack of information. However, effects of catastrophes may be easily incorporated into a baseline model and sensitivity analysis. For simplicity, we assumed that environmental stochasticity was lognormally distributed.

Correlations among populations in vital rates

Inter-annual variability in carrying capacity, survival rates and fecundity can be correlated among discrete populations when environmental or other factors influence population dynamics in similar ways across part or all of a region. Because populations in our study area are influenced by some environmental processes that occur over regional scales, but fall within a complex network of channels and inlets subject to different environmental processes over smaller scales (e.g. freshwater influx) we assume a 0.5 correlation among populations in our baseline scenario, although the true level of correlation among populations is unknown. In our sensitivity analyses, the degree of correlation in K, transition probabilities and fecundity varied from 0 to 1 by sampling from a uniform distribution.

3.2.3.3. Dispersal Model

At each time step *t* in our model, larvae are born, survive, and then disperse. The degree to which larvae disperse from natal populations and the distances they travel prior to settlement onto benthic substrata are unknown in *P. californicus*, as is the case for most marine invertebrate species. This is a perennial issue in models that simulate the dynamics of spatially structured populations in marine systems. Typically, such models apply a simple dispersal kernel (e.g. a Laplacian dispersal probability density function) to predict the probability of larvae being transpoted a specified distance away from the source population (e.g. Botsford et al. 2009; Pepino et al. 2012). Such dispersal kernels have been applied in similar studies to evaluate reserve design. However, our study system is characterized by a complex network of inlets and channels (Figure 3-1). This poses significant computational challenges for implementing simple dispersal functions such as Laplacian dispersal because movement of larvae are constrained to the network of channels and inlets, while simple dispersal kernels typically assume that the probabilities of dispersing in any given direction are equal.

One alternative to dispersal kernels is to simulate the movement of larvae using a model of ocean circulation (Robinson et al. 2005). In such simulation models, the movement of larvae are either simulated assuming that they behave like particles that drift passively with currents and tides, or the movement of larvae exhibit simple behaviours such as diel migrations, phototaxis, chemotaxis, or aggregation. This approach requires the development (or availability) of a model of the circulation patterns of water within the study area. Even when such models are available, simulating particle movements and analyzing results can be computationally intensive (Foreman et al. 2009). However, simulating particle movements can be more informative than simple dispersal kernels as the latter tend to ignore the influences of currents, winds, and tides as well as larval behaviour. An ocean circulation model is available for PFMA 12, and was one of the reasons the study area was selected for this case study. However, unavoidable delays and time constraints prevented the inclusion of the results of the circulation model in the present analysis. However, our tool has the flexibility of incorporating output from a variety of dispersal models or empirical field studies, provided that the outputs are expressed as probabilities of dispersal amongst population pairs.

To simulate dispersal in our network of channels and inlets in this paper, we assume that the per unit area dispersal rate from population *i* to population *j* is equal for all population *j* that are within a threshold distance of population *i*, D_{max}, where the distance between pairs of

populations (i.e. pairwise distance) is calculated as the minimum distance larvae must travel through the network to arrive at population *j*.

To calculate dispersal rates, we first calculate the distances between each pair of populations in the study area as described above and construct a matrix of pairwise distances. The matrix of pairwise distances between all habitat patches was calculated using GIS software. The distance between patches was measured from a single point placed within each habitat patch. The point was not necessarily located in the center of the habitat patch, as the centroid sometimes fell outside the patch (e.g., on land or an area of unsuitable habitat). The location of each point is determined using the *genpointinpoly* function (position = LABEL) in the Geospatial Modelling Environment software (version 0.7.1.0) (Beyer 2012). Distances between the points were calculated using a 300x300 m cost distance raster created for each habitat patch. The cost distance rasters are calculated using the cost distance tool in the Spatial Analyst extension of ArcMap 10.0 (ESRI 2011). Land barriers were considered in the cost distance raster to the greatest extent possible. However, twelve narrow land barriers could not easily be removed. The maximum potential error in pairwise population distance calculation for these land barriers ranged approximately from 2 to 13 km (mean = 6.8 km). The actual errors caused by these barriers are much smaller than the maximum potential error, and do not affect all pairwise distances. The errors caused by not taking these land barriers into account is unlikely to affect results because patch size was generally larger than these distances and the mean distance between the habitat patches was an order of magnitude larger (mean = 59 km). In future applications of these tools, uncertainties associated with land barriers could be reduced.

In our baseline model we assume that larvae are capable of dispersing up to 30 km (= D_{max}) during the course of their pelagic stage (51-120 days). This value and range was based on the mean larval dispersal distances of several invertebrate species (Shanks et al. 2003; Siegel et al. 2003; Shanks 2009).

We then construct a matrix of pairwise dispersal rates which represents the proportion of larvae that disperse from the i^{th} population to the j^{th} population, m_{ij}, at each time step. If a pair of populations falls within the threshold distance, a dispersal rate is calculated and we refer to that pair of populations as being connected. For each population *i*, we identify all of the neighbouring populations that fall within the threshold distance, D_{max}, and calculate m_{ij} as the inverse of the total number of populations connected to population *i* weighted by each population's area. In this manner, larvae have an equal per unit area probability of settling in their natal population *i* as they do in any of the population *j*s connected to population *i*. Stochasticity in dispersal rates is introduced by randomly varying the rates at each time step assuming a 10% coefficient of variation (CV). Dispersal rates are assumed to be independent of the densities of sea cucumbers in populations *i* and *j*.

Given uncertainty in the dispersal patterns of larval *P. californicus*, we vary the threshold distance, D_{max}, across the range of plausible values in our global sensitivity analysis, which includes two special cases. In the first special case we assume that there is no dispersal from any population *i*, such that no pairs of populations are connected and all larvae recruit to their natal populations (i.e. $D_{max} = 0$). In this case, the m_{ij} are all equal to 0 and each population retains 100% of its surviving larvae. In the second special case we assume that D_{max} is infinitely large, populations are equally connected such that larvae from population *i* are as likely to settle in cells within their natal populations as they are to settle in cells within any other population within the study area. Thus m_{ij} is simply calculated as the inverse of the total number of populations weighted by their areas. Once all of the m_{ij} are calculated, the matrix of pairwise dispersal rates is imported into the RAMAS Metapop file (*.mp) using customized GRIP code. Thus, the dispersal matrix can be generated externally using any dispersal model specified by the user. Users can now read in a dispersal matrix created using any external model (e.g. ocean

circulation model, Laplacian dispersal kernel), provided the matrix elements are expressed as proportions of larvae dispersing from population *i* to population *j*. Code could be modified to randomly import one of multiple dispersal matrices based on alternative dispersal models in order to assess the influence of dispersal model assumptions on simulation results. Users can also weight dispersal rates by patch area. This allows users to consider the influence of simple assumptions about dispersal patterns.

In GRIP 1, once dispersal rates are generated by the dispersal model, they are randomly varied to assess their relative influence on model predictions. For simplicity, this functionality was turned off. Dispersal mortality was set to zero in this version of GRIP because it was incorporated into estimates of larval survival when constructing the stage matrix. Both of these functions remain in the code. In addition, the CSV file now records the mean proportion of larvae leaving natal populations and the mean pairwise dispersal rates. Also, our customized code no longer assumes that dispersal rates are symmetrical among populations.

3.2.3.4. Fisheries Management Model

Population dynamics and fisheries management occur at different spatial scales. Our study area, Pacific fishery management area (PFMA) 12 is subdivided into Pacific fishery management (PFM) subareas (Figure 3-5), and each of these can include zero, one or multiple patches of suitable habitat or populations. In our simulations, each population falls within a single PFM Subarea. While metapopulation dynamics are simulated at the patch scale, sea cucumber fisheries management is generally implemented at the scale of subareas or groups of subareas called quota management areas (QMAs). Two types of fishing events are simulated: commercial harvest and other harvest (i.e. First Nations or recreational). Commercial harvest was simulated within populations that fall outside the FCAN. Other harvest was implemented concurrently with commercial harvest but only in populations that were part of the FCAN.

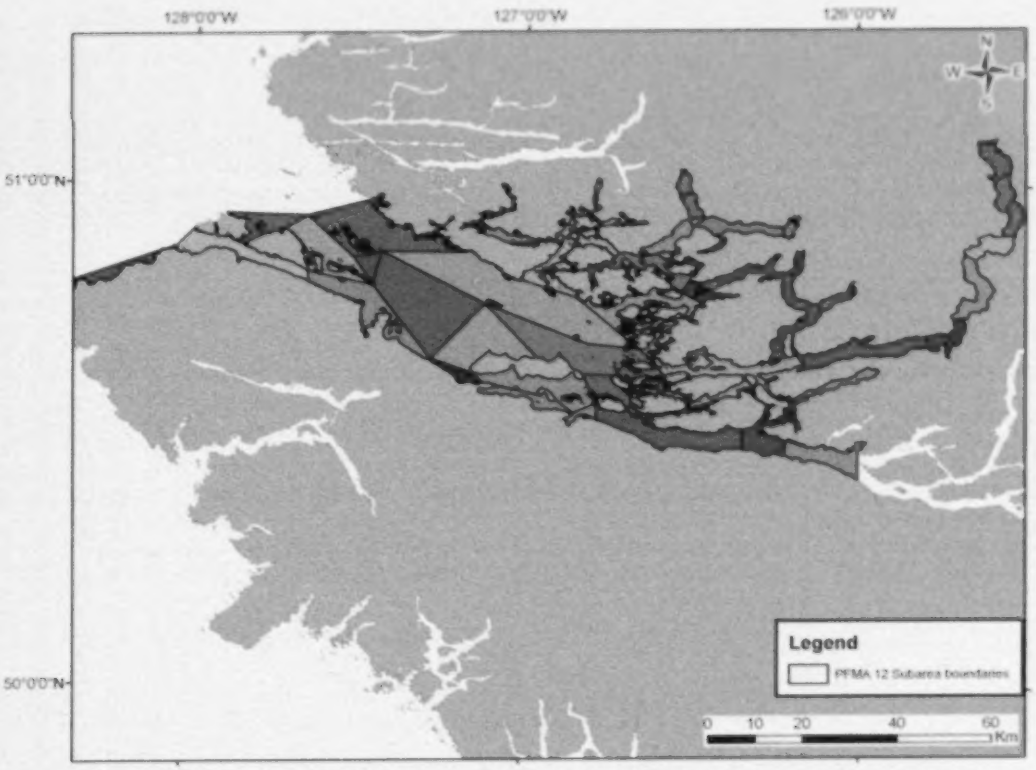

Figure 3-5: The Subarea boundaries of Pacific Fisheries Management Area (PFMA) 12. The different colours represent the different subareas within the PFMA.

Currently the *P. californicus* commercial fishery is managed through an annual Integrated Fishery Management Plan (IFMP) that specifies the allowable catch by time and location. The IFMP implementation commences on October 1st and ends the following September 30th. Commercial fishery quotas are calculated for each open Pacific Fishery Management (PFM) Subarea (see Duprey et al. 2011 for methods of how each PFM Subarea is assessed). The annual harvest rate used in calculating quotas is based on recommendations made in Hand et al. (2009) and is 4.2% or 6.7% of the estimated biomass depending on the PFM Subarea. Recently, management of the commercial fishery has shifted from all open PFM Subareas being harvested annually to developing a 3-year rotation, where PFM Subareas are harvested once every three years at a harvest rate of 10%. This rotational scheme is still being finalized and it may take several more years to fine tune how the rotation schedule will function with all the open PFM Subareas throughout BC, but the current plan is to move the commercial fishery in that direction.

In the fisheries management structure of the FCANs described in this analysis, populations of *P. californicus* that are a part of the FCAN are closed to commercial fishing, but remain open to other forms of harvest (i.e., recreational and First Nation). However, other forms of harvest are not simulated in areas that are open to commercial fishing. This section describes the three key components in our fisheries management model that specify

1. the location of areas closed to commercial fishing;
2. the location, frequency, and intensity of commercial harvest, and;

3. the location, frequency, and intensity of other types of harvest.

In our baseline model we use the existing management structure for PFMA 12 that defines the location, frequency and intensity of commercial harvest. In our global sensitivity analysis we vary the size, number, and location of FCANs as well as harvest parameters to explore the influences these factors have on our capacity to achieve multiple management objectives. In the following sections we describe the three components of the fisheries management scenarios and the parameters used to build our baseline fisheries management model. In subsequent sections we describe the management objectives used to evaluate the performance of alternative FCAN designs and methods used in our global sensitivity analyses to explore the influence of FCAN attributes on our ability to meet management objectives.

3.2.4. Areas included in the FCAN

In the baseline model, subareas that are currently closed to commercial fishing are treated as being part of an FCAN. Our study area largely represents PFMA 12 (Figure 3-5), which is subdivided into 48 PFM Subareas, but it does not include PFM Subarea 12-25. All populations within a PFM Subarea are either open or closed to commercial exploitation. In the baseline model, PFM Subareas 5, 6, 12, 14, 15, 18, 19, 25, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 42, 43, 44, 45, 46, 47, and 48 are closed to fishing. For the remaining PFM subareas where commercial fishing takes place, the scheduling of rotational openings for commercial harvest is established by quota management area (QMA), each of which comprises one or more PFM subareas (see Table 3-5 for scheduling of commercial rotations). PFM Subareas can be closed for one of three reasons:

1. the density falls below the management threshold for harvest (2.5 sea cucumbers per meter of shoreline);
2. they have not been surveyed; or
3. they are current no-take areas.

Table 3-5. Quota Management Areas (QMA) are groupings of PFM Subareas used to manage total allowable catches (TACs). There are four QMA located within Pacific Fisheries Management Area (PFMA) 12. The PFM Subareas located within each QMA are listed with the anticipated schedule of openings to commercial fishing (Rotation years).

QMA	Name	3yr Harvest Rate	Years Open	Subareas
12A	N. Queen Charlotte Strait	10%	2012, 2015, 2018, 2021, 2024,...	12-9 to 12-11, 12-13, 12-16
12B	S. Queen Charlotte Strait	10%	2013, 2016, 2019, 2022, 2025,...	12-7, 12-8, 12-17, 12-40, 12-41
12C	Johnstone Strait	10%	2011, 2014, 2017, 2020, 2023,...	12-1 to 12-4, 12-21 to 12-24*
12D	Gilford Island	10%	2013, 2016, 2019, 2022, 2025,...	12-20, 12-26, 12-38, 12-39

In our sensitivity analysis, we explore the influence of spatial management scale by either implementing closures at the PFM subarea scale, or at the population scale. To achieve this, we modified GRIP code to vary the scale at which FCANs are managed (i.e. subarea or population), and code to vary which subareas and populations are part of the FCAN in each scenario. Populations are selected to be part of the FCAN on either the PFM Subarea scale (as in the baseline scenario) or they are selected individually at the population level (e.g., not all populations in a PFM Subarea are necessarily closed). The first step in the code is to randomly select the spatial management scale (subarea or population). If management occurs at the PFM subarea scale, the number of areas included in the FCAN are selected from a uniform distribution ranging from 1–47 (the number of PFM Subareas in the study area), and commercial harvest is closed in all the populations that fall within those subareas. If management occurs at the population scale, the number of populations included in the FCAN is randomly selected from a uniform distribution ranging from 1–370 (Table 3-6), and commercial harvest is closed in those areas. Once the number of PFM subareas or populations has been selected, the areas or populations to be included in the FCAN are randomly drawn from the set with equal probabilities. By virtue of randomly varying which subareas or populations are included in the FCAN, we randomly vary a number of other FCAN metrics (e.g. total shoreline, total area, pairwise population distance) which we can use to evaluate the relative influences of FCAN attributes on model predictions.

3.2.5. Commercial fisheries

While fisheries management parameters have been incorporated into GRIP in previous studies (Curtis and Vincent 2008), we added the capacity to simulate two types of fishing pressure, so that we could implement commercial and other harvest concurrently. In both types of fishing, users can specify distributions for harvest rates and implementation uncertainty. Note that other types of fisheries management could easily be incorporated into our analyses, including size limits, supplementation and translocation, while the range of harvest rates can be varied easily in sensitivity analyses.

In our baseline scenario, we use the existing commercial harvest management regime implemented in PFMA 12. Harvest occurs every three years (rather than annually) with an exploitation rate of 10% of the population estimated in year 0. Due to financial constraints and geographical extent of the *P. californicus* fishery, biomass surveys of the same areas are not repeated regularly. Therefore, the current practice in fisheries management is to estimate the population abundance before opening a PFM Subarea, setting a TAC for each PFM Subarea, and applying this TAC in subsequent years, until a new survey of the PFM Subarea can be completed. Therefore, for our simulations the total number of adults harvested from each population during each harvest event is fixed throughout the time horizon of the simulation. Although subsequent surveys are likely to occur over long time horizons, estimating when these new surveys would occur is difficult and no attempt was made to do so in the baseline and sensitivity analysis.

In our sensitivity analysis the frequency of harvest and exploitation rates are varied. Commercial harvest in PFMA 12 is currently managed on a three year rotation. However, some PFMAs in BC are commercially harvested every year. In those areas the annual harvest rate is set at 4.2%. Because two different harvest frequencies are utilized in BC, they were both tested in the sensitivity analysis. In both scenarios, a range of exploitation rates were implemented in the sensitivity analysis to test plausible changes to management harvest goals. Harvest rates were randomly sampled from a normal distribution around the current management harvest rates (4.2% for 1-year rotation; 10% for 3-year rotation) with a coefficient of variation (CV) of 5% (Table 3-6).

In both our baseline and sensitivity analysis simulations, two modifications were made to the harvest rate to incorporate uncertainty. First, we adjusted the harvest rate to better reflect how the harvest rate is implemented. In practice, commercial harvest rates are applied to the 90% lower confidence bounds (LCB) of the bootstrapped estimate of the population size (Duprey et al. 2011, Duprey 2011, 2012). The presented simulation tool estimates mean population abundance, not the 90% LCB of the population abundance. If the above harvest rates were to be applied to the mean population estimate used in the simulator, the results would not be accurately replicating the management regime currently in place for the fishery. Therefore, a correction factor was developed to adjust the harvest rate so it could be applied to mean population abundances. Using the survey data collected and analyzed for PFMA 12 (Duprey 2012; N. Duprey, Fisheries and Oceans Canada, Nanaimo, BC, unpublished data) a correction factor was calculated to compensate for the difference between the 90% LCB and the mean population estimates. The 90% LCB was found to be 66% of the mean estimate. Therefore, a 0.66 harvest rate correction factor was set for all Subareas within PFMA 12. After the application of the correction factor the harvest rates for the annual and 3-year rotational fishing regimes used in the simulator were 2.8% and 6.7%, respectively. In either scenario, target harvest rate and frequency were constant throughout the duration of the time horizon. However, we assumed there was uncertainty associated with implementation of TACs within PFM Subareas (Table 3-5). To incorporate this into our model we added some stochasticity to the actual proportion of the population harvested. Therefore, the number of individuals harvested from population i at time step t ($C_{i,t}$) was calculated using the equation:

$$C_{i,t} = 0.066 \cdot \hat{N}_{i,t}$$

where $\hat{N}_{i,t}$ is drawn from a normal distribution with mean $N_{i,t}$ and standard deviation $N_{i,t}$ 0.05 (i.e. 0.05% CV).

3.2.6. Other fisheries

Currently, areas closed to commercial harvesting of *P. californicus* are still open to other forms of harvesting, such as recreational and First Nation food, social, and ceremonial (FSC) harvest (hereafter consolidated into Other Exploitation Rate, OER). For this analysis Fisheries Management requested that FCAN designs be structured to include OER in areas that are closed to commercial fishing. Landings of *P. californicus* are not currently recorded for recreational or First Nation FSC harvests. Therefore without landing data for these types of exploitations Fisheries Managers were asked to provide their best estimate of the amount of the population being exploited by these user groups. In our baseline scenario, Fisheries Management indicated that an appropriate annual OER of 0.75% be simulated to account for these types of removals (P. Ryall, Fisheries and Oceans Canada, Vancouver, BC, personal communication). As with the calculations of the commercial harvest rate, a correction factor of 0.66 was applied to this estimate to reflect the fact that management calculates TAC according to the 90% LCB of the initial biomass estimate. Therefore, the annual OER harvest rate used in the simulator is 0.50%. In each scenario, target harvest rate and frequency were constant throughout the duration of the time horizon. However, we assume that there is uncertainty in estimates of abundance in population i at time $t = 0$ (N_i) due to sampling error as well as uncertainty associated with the implementation of TACs within PFM Subareas. Thus the actual number of individuals harvested in FCANs from population i at each time step t (C_i) is given by the equation:

$$C_{i,t} = 0.005 \cdot \hat{N}_{i,t}$$

where N_t is drawn from a normal distribution with mean N_t and standard deviation $N_t \cdot 0.05$ (i.e. 5% CV).

3.2.7. Modeling time horizon

The dynamics of metapopulation models during the first time steps are typically driven by initial conditions (Pe'er et al. 2013). Therefore we allow the model to run for 20 time steps (years) prior to implementing fisheries management scenarios. Results are shown from time step 20 to 120 simulating 100 years of fisheries management, starting in 2011 (see Table 3-5 for schedule of rotation in PFMA 12).

Table 3-6. Model parameters that may be varied in a sensitivity analysis

Parameter	Baseline Value	Range Used in Sensitivity Analysis	Assumptions	Varied in this paper
Habitat suitability threshold	0.75	0.7, 0.75, 0.8, 0.9	Habitat with suitability values greater than the defined threshold are assumed to be of sufficient quality to support survival, growth, reproduction and movement	No
Neighbourhood distance	850 m	600m, 850m, 1450m, 1700m	Used to define the spatial structure of discrete populations linked by dispersal	No
Fecundity	30	15 – 45 (sampled from a uniform distribution)	Population is at or near equilibrium abundance	Yes
$\theta_{1,0}$	0.2	Sampled from lognormal distribution with CV = 20%	Small juveniles more vulnerable to predation than larger juveniles and adults	Yes
$\theta_{2,0}$	0.2	Sampled from lognormal distribution with CV = 20%	Small juveniles more vulnerable to predation than larger juveniles and adults	Yes
θ_{3+}	0.69	Sampled from lognormal distribution with CV = 20%	Large juveniles have same survival rate as adults	Yes
θ_{m}	0.5	Sampled from lognormal distribution with CV = 20%	Juveniles mature between 5-8 years of age	Yes

Parameter	Baseline Value	Range Used in Sensitivity Analysis	Assumptions	Varied in this paper
ϕ_{im}	0.19	Sampled from lognormal distribution with CV = 20%	There is a staged progression from juvenile to adult	Yes
ϕ_{ad}	0.69	Sampled from lognormal distribution with CV = 20%	Sea cucumbers live approximately 12-14 years.	Yes
Models of Density-Dependence	Beverton-Holt	Beverton-Holt Ricker Ceiling model	Density influences survival and fecundity of large adults	No
R_{max}	1.27	1.05 – 1.29	Baseline estimates are taken from stock assessments of related species.	Yes
K	Based on predictions of adult density, mean density * area of suitable habitat	Sampled from a normal distribution with CV = 10%	Surveys were carried out when population is at or close to equilibrium; density model is correct	Yes
Standard Deviation in K	CV = 10%	CV in K is sampled from a normal distribution with mean = 0.18, SD = 0.09	Based on estimates of annual variation in abundance in unfished sites. May be over-estimated due to sampling error.	Yes
Initial Abundances	Based on predictions of adult density, mean density * area of suitable habitat	Vary independently for each population with CV = 10%	Habitat model is correct; assume stable age structure at time = 0	Yes
Correlations among	0.5	Sampled from uniform distribution.	A value of 0 means that populations are uncorrelated in survival	Yes

Parameter	Baseline Value	Range Used in Sensitivity Analysis	Assumptions	Varied in this paper
populations		0-1	rates, fecundity and K among years, while a value of 1 means they are perfectly correlated	
D_{max}	30 km	Vary from 0 to 300 km, sampling from a uniform distribution	Fit oceanographic model output to dispersal-distance function; larvae move passively	Yes
Scale of fisheries management	PFM Subarea	Randomly sampled either PFM Subarea or population		Yes
Number of PFM Subareas in the FCAN	25	Sampled from a uniform distribution, 1-40		Yes
Number of populations in FCAN	150	If managed at population scale, sampled from a uniform distribution, 1 - 370		Yes
Commercial harvest rate (3-year rotation)	6.6%	Sampled from a normal distribution with CV = 5%	Used when there was a 3-year rotational harvest	Yes
Commercial harvest rate (annual)	2.8%	Sampled from a normal distribution with CV = 5%	Used when there was annual harvest. This was only used in the sensitivity analysis, not used in the baseline	Yes
Other Exploitation Rate	0.50%	Sampled from a normal distribution with CV = 5%		Yes
Commercial harvest frequency	Every three years	Randomly sample either 1 or 3 years		Yes

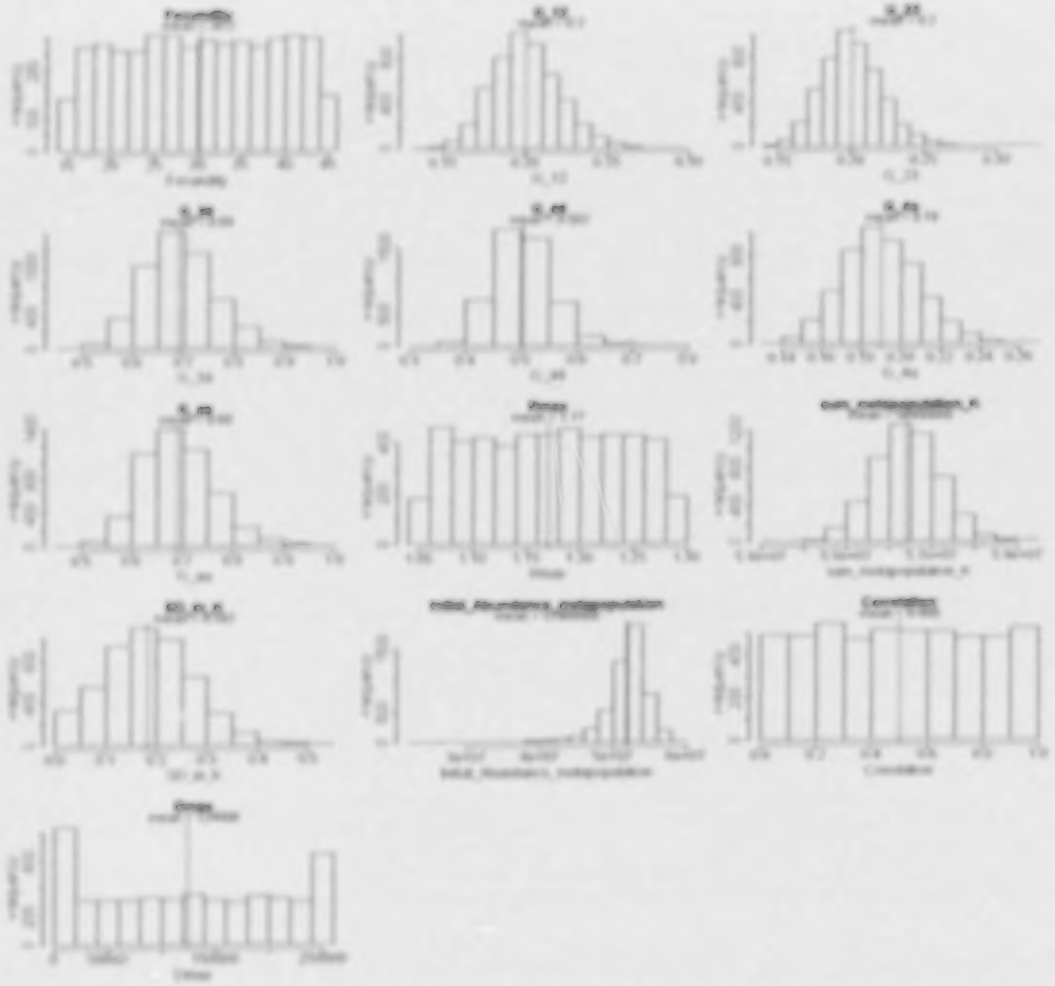

Figure 3-6. Distribution of biological input parameters used in the sensitivity analysis. The mean is indicated with a red vertical line.

3.2.8. FCAN metrics

In addition to the number of PFM Subareas or populations included in the FCAN, a variety of metrics related to the size and structure of each of the simulated FCAN designs was included in the sensitivity analyses. By virtue of randomly varying populations that are included in the FCAN, we also randomly vary the area, spacing, carrying capacity, connectivity, and shoreline length associated populations in FCANs. By exploring relationships between these parameters and our performance criteria, we can identify potential attributes of FCAN design that could be managed to help achieve management objectives.

The first set of metrics relates to the length of shoreline included in the FCAN. Shoreline length included in the FCAN is of particular interest in the case of the *P. californicus* fishery as it is currently managed based on the number of sea cucumbers per meter of shoreline rather than by density of cucumbers per meter squared. Two separate metrics were calculated:

1. the length of shoreline included in the FCAN; and
2. the proportion of shoreline in the study area included in the FCAN.

The length of shoreline affected by each of the 370 populations was estimated using ArcMap 9.2. Population polygons (which included both areas of suitable habitat and the neighbourhood distance buffers; see Section 3.2.3) which were overlaid on the shoreline map used by Fisheries Management to measure the shoreline length of each PFM Subarea (Duprey et al. 2011). The base layer maps used to create the population polygons are more accurate low mean water shoreline representations than the fisheries management file and were created using different projections. Therefore the two maps did not overlay perfectly and simple rules were needed to estimate the amount of affected shoreline (the amount of shoreline in the fisheries management shoreline map affected by population polygons used in modeling) in the fisheries management shoreline. For all populations, lines were drawn from the edges of their polygon perpendicular to the fisheries management shoreline to mark the start and end locations of where the two overlapped. For a segment of shoreline to be deemed affected by an population polygon it had to be a perpendicular distance of 600 m from the population's polygon and be located within the same PFM Subarea. Population ploygons that did not have any shoreline meeting these criteria were given an affected shoreline length of zero. A small number of populations were located on land due to the poorer spatial accuracy of Fisheries Management's sea cucumber shoreline compared to the shoreline files used to create the populations. These populations were given an affected length of one meter. The length of all affected segments of shoreline was then summed for each population.

The first shoreline metric, the length of shoreline included in the FCAN, was calculated by summing the amount of affected shoreline for each of the populations included in the FCAN. The second shoreline metric, the proportion of shoreline included in the FCAN, was calculated in two ways, depending on whether areas were included in the FCAN by PFM Subarea or by population. If areas were included in the FCAN by PFM Subarea, the entire shoreline length of each PFM Subarea was summed and divided by the shoreline length of the entire study area. If areas were included in the FCAN by population, the length of all populations included in the FCAN were summed and divided by the entire shoreline length in the study area.

The second set of metrics relates to the amount of area contained within the simulated FCAN. Two separate, but closely related, metrics were calculated:

1. the area of suitable habitat included; and
2. the total area (suitable habitat plus neighbourhood distance buffer, see Section 3.2.1) included in the FCAN.

Both of these metrics were calculated at the population level rather than the PFM Subarea level regardless of how areas were included in the FCAN.

The total affected shoreline length of all the populations was 2,375,473 m (75.3 % of the shoreline in PFMA 12); the total area of all the populations was 975.25 ^{2} (32 % of the area of PFMA 12).

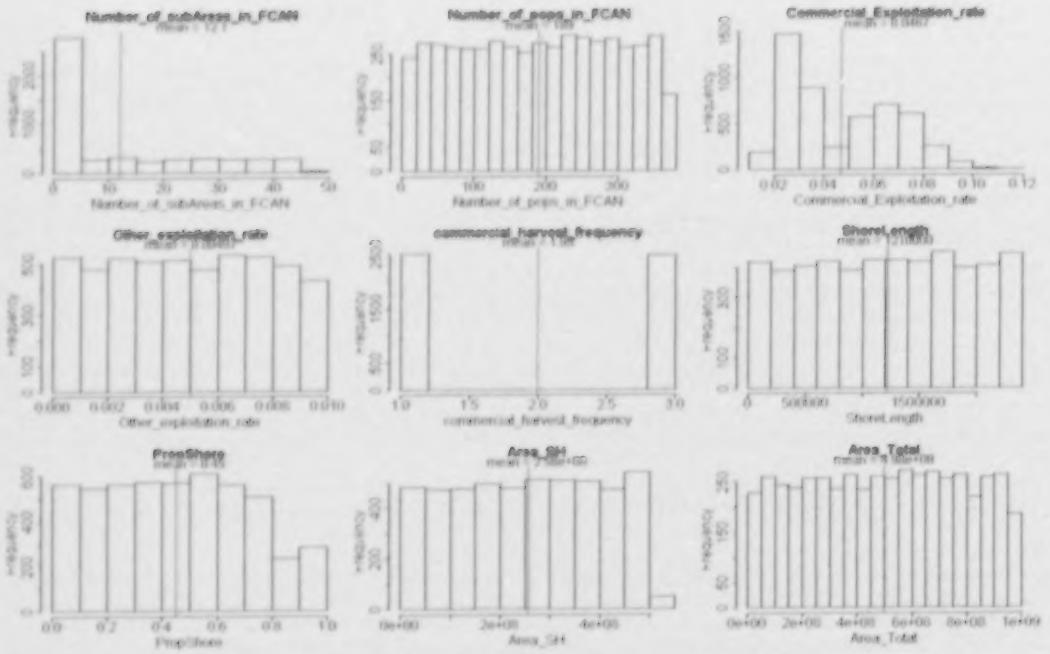

Figure 3-7. Distribution of management input parameters used in the sensitivity analysis. The mean is indicated with a vertical, red line. Commercial exploitation rate has two modes due to annual and 3-year rotational harvest regimes occurring in the same histogram.

3.3. ANALYSIS

3.3.1. FCAN performance metrics

Several metrics were calculated to evaluate the ability of each simulated FCAN to meet conservation and management objectives for both the baseline scenario and each scenario in the sensitivity analysis. The percent decline of the metapopulation from the unfished biomass was calculated at 20 and 100 years, as:

$$PercentDecline = \left(1 - \frac{B_t}{B_0}\right) \bullet 100$$

where B_0 is the biomass at t = 0 (unfished biomass, corresponding to 2010 in our simulations), and B_t is the biomass at t = 20 or 100. In cases where populations increase the percent decline was set to zero. Percent decline is broadly used to assess extinction risk (IUCN 2001).

To quantify the influence of model parameters on our ability to achieve specific fishery management objectives, we customized GRIP code to calculate two new metrics related to management objectives:

1. the number of subareas that fell below a specified limit reference point (LRP) in year 20 or year 100, and
2. the proportion of years in which at least one subarea fell below the LRP over 20 or 100 years.

In our case, the LRP was 50% of original biomass. The number of PFM Subareas below the LRP was calculated using the following formula:

$$N_{Subareas<LRP} = Count(Subareas < LRP)$$

at both 20 and 100 years. The proportion of all years in the time horizon where at least one PFM Subarea was below the LRP was calculated as:

$$P_{YearsAtLeastOneSubarea<LRP} = \frac{Count(YearsAtLeastOneSubarea < LRP)}{t}$$

Where t is either 20 or 100 years. Note that additional performance metrics related to the distribution or abundance patterns of individuals could be programmed into the code. The LRP, time horizon and spatial scale at which metrics are calculated can be easily modified in GRIP.

3.3.2. Boosted regression tree analysis for variable importance

Boosted regression tree (BRT) analysis was conducted on the sensitivity analysis scenarios to determine the relative importance of various input parameters in meeting conservation and management objectives. See Section 2 for a full description of BRT analysis. In this context, the various biological and management input parameters were used as the predictor variables, and the FCAN performance metrics were used as the response variables.

The same methods described in Section 2 were used to build BRT models for the simulator sensitivity analyses, with one important exception. Due to time constraints, it was not possible to optimize the parameter settings for the BRT analysis, and default settings in dismo were used. The default settings for learning rate (lr), bag fraction (bf), and tree complexity (tc) are 0.1, 0.75, and 1, respectively. A tc of 1 means that interactions were not modeled. While there are likely to be important interactions between variables such as harvest rate and number or area of subpopulations in the FCAN, we did not investigate interactions due to time constraints. Future analyses of simulation output should fully explore the role of interactions that might inform management decisions. As with the analysis in Section 2, all models were built and analysed in R (R Development Core Team 2011) version 2.14.1 using the packages gbm version 1.6-3.2 (Ridgeway 2012) and dismo version 0.7-17 (Hijmans et al. 2012).

3.4. RESULTS

3.4.1. Baseline simulation results

IMPORTANT NOTE: the following discussion of results is for illustrative purposes only, it is meant to give an idea on how interpretation could proceed with simulations outputs. In some parts a full analysis was not completed, however these results do give much insight into how results would be used for interpretations.

A total of 1,000 stochastic runs were used in the simulation of our baseline scenario, which represents our best approximation of biological parameters and the current management regime. Output from the baseline runs of the simulator show *P. californicus* populations, in PFMA 12, experience mean declines of 2.95 % after 20 years and 2.90 % after 100 years (Figure 3-8). No PFM Subareas were below the LRP at 20 and 100 years, therefore the proportion of PFM Subareas below LRP over 20 and 100 year time horizons was 0.

Our results suggest that the productivity of populations may be sufficient to support the current harvest rate. However, two key assumptions of our baseline model influence how populations respond to harvest. The first assumes that populations are at equilibrium prior to the onset of fishing, which means in the absence of fishing, density-dependence, dispersal, stochasticity,

and other drivers of population change, the populations are expected to remain at the initial abundance. The second assumes that as populations decline, productivity will increase through compensatory increases in survival and/or fecundity. This is a property of the Beverton-Holt model used to simulate density-dependence in population growth, and a common assumption in fisheries models. The degree to which productivity increases is a function of R_{max}, which in our model is 1.27, i.e. populations can grow up to a maximum of 27% per time step when abundance is low. Thus compensatory density-dependence counteracts the effects of population decline associated with harvest. With an assumed Beverton-Holt model governing density-dependence in our baseline model, an R_{max} of 1.27 and a range of 1.05 to 1.30 explored in our sensitivity analyses, the maximum population growth rate at each time step exceeded the harvest rate averaged among years in all scenarios. Future simulations that explore the influence of alternative models of density dependence (i.e. Ricker, Ceiling) would be useful in the context of informing conservative fisheries management decisions.

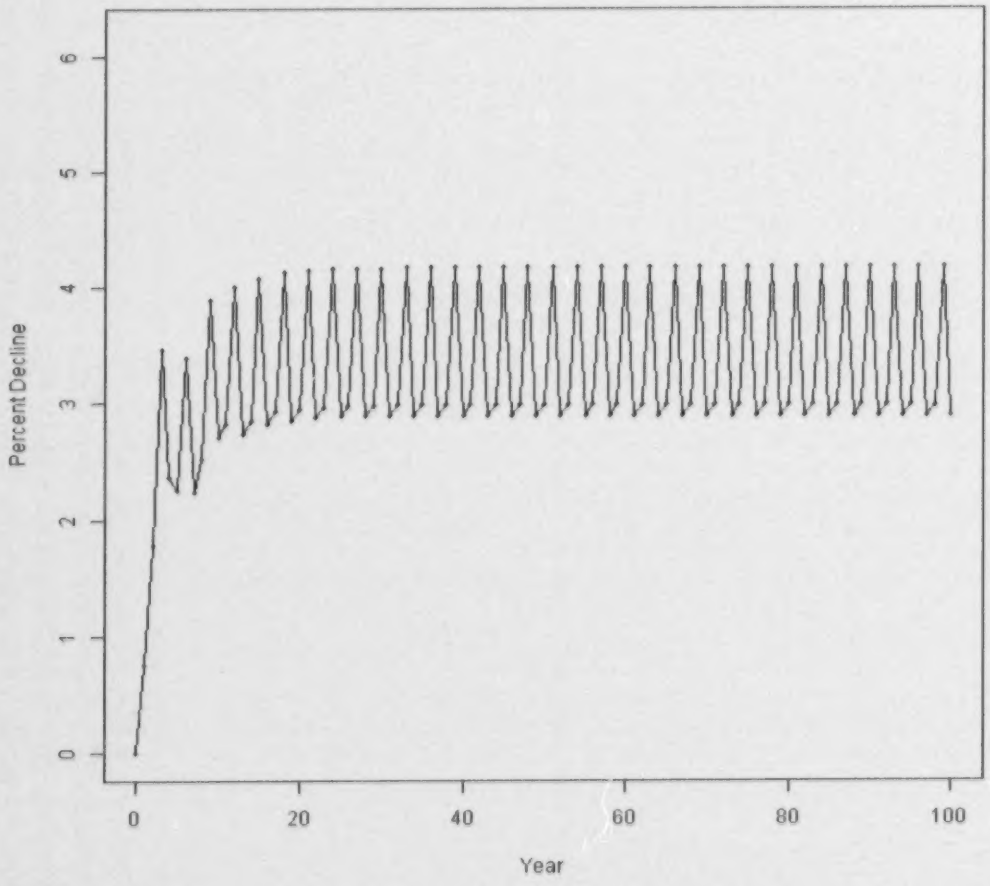

Figure 3-8. The mean percent decline of 1,000 stochastic runs over a 100 year period.

3.4.2. Sensitivity analysis

A total of 29 variables, both continuous and categorical, were randomly and independently varied in 5,000 scenarios in order to test the sensitivity of the simulator outputs to varying inputs

(Table 3-6 for a list of the 29 variables) and to evaluate their relative influence in achieving the conservation and management objectives. With 5000 unique sets of input parameter values explored in our scenarios, we were able to sample a considerable portion of the parameter space. However, scenarios explored in this manner are influenced by the distributions from which parameters are drawn. For instance, parameter values drawn from a normal distribution will tend to cluster around the mean, while those drawn from uniform distributions will be more evenly represented across the parameter space. In our case, we focus on analysis of scenarios that cluster around our baseline model which represents the best available information on habitat, dispersal, population dynamics and fisheries management. Scenarios that include parameter values drawn from the extreme ends of probability distributions are deemed less likely to occur and of lesser concern for informing decisions on FCAN design. The potential influences of parameter ranges and probability distributions specified in future sensitivity analyses should be considered in relation to study objectives.

For the purposes of this study, Fisheries Management indicated that one of their objectives was to ensure population did not decline below 50% of the initial biomass at 20 and 100 years. They also requested information on the number of PFM Subareas below LRP at 20 and 100 years, and the proportion of years where at least one PFM Subarea was below LRP over the 20 or 100 year time horizon. Therefore, the results of the sensitivity analysis are broken down according to those three performance metrics.

Metapopulation Percent Decline

The performance metric that provided the most information on the relative performance of difference FCAN scenarios explored in the sensitivity analyses was percent metapopulation decline (i.e. percent decline). The mean percent metapopulation decline across all sensitivity analyses scenarios was 4.46% and 4.72% at 20 and 100 years, respectively.

Boosted Regression Tree (BRT) analysis was carried out to rank the relative influence each of the 29 input variables had on metapopulation percent decline at 100 years. The three most influential variables in the BRT analysis were Standard Deviation in K (49.88 %), Initial Abundance of the Metapopulation (34.39 %), and Shoreline Length of an FCAN (3.32 %). The relative influences of all variables are listed in Table 3-7, and the results of some of the more influential variables from the BRT are presented below. Variables are divided into two categories based on the degree of control fisheries managers have in manipulating their values:

1. Biological Variables (managers have no control); and
2. Management Variables (managers have control through management action).

Number of PFM Subareas Below LRP

Of the 5,000 FCAN scenarios in the sensitivity analyses, only 4 (0.08%) had one or more PFM Subareas below LRP at 20 years, and 24 (0.48%) at 100 years. Since the LRP was rarely surpassed, this indicates that the current management regime is likely maintaining populations above the LRP and therefore the development of a FCAN for PFMA 12 may have limited influence on the risk of exceeding the LRP over short (20 year) or long (100 year) time frames, given the current management regime and key assumptions in our simulator.

Proportion of Years in Which at least One PFM Subarea is Below LRP during the time horizon

Of the 5,000 scenarios in the sensitivity analyses only 9 (0.18%) and 43 (0.86%) scenarios had a PFM subarea fall below the LRP during the 20 and 100 year time horizons, respectively. As with the previous performance metric, the LRP was rarely surpassed. Thus our simulations predict that the current management regime is likely to maintain populations above the LRP throughout the assessed time frames (20 and 100 years). Therefore this result also supports

the conclusion that if the current management regime was to continue under the same assumptions built into our simulator, the development of an FCAN for PFMA 12 may have limited benefits in terms of reducing the risk of exceeding the LRP during short (20 year) and long (100 year) time frames.

Table 3-7. Relative influence of variables varied in the sensitivity analysis.

Variables	Relative influence (%)
Standard Deviation in K (SD in K)	49.88
Initial Abundance Metapopulation	34.39
Shoreline Length (ShoreLength)	3.32
Total Area of FCAN (Area)	2.80
Suitable Habitat Area (Area_SH)	2.30
Commercial Exploitation rate	1.08
Commercial Harvest Frequency	0.89
Correlation	0.88
Survival - Adult (G_aa)	0.86
Number of Populations in FCAN	0.85
Other Exploitation Rates	0.72
Proportion of Shoreline in FCAN (PropShore)	0.66
Mean Connected Distance	0.63
Mean Population K	0.31
Fecundity	0.29
Rmax	0.07
Survival - Proportion of Year 4+ remaining juvenile (G_44)	0.06
Dmax	0.01
Survival - Year 1 to 2	0.01
FCAN designed at PFM Subarea or Population scale	0.00
Number of PFM Subareas in FCAN	0.00
Sum of Metapopulation K	0.00
Dispersal Scenario	0.00
Mean Proportion Dispering	0.00
Mean Pairwise Dispersal Rate	0.00
Connectivity	0.00
Survival - Year 2 to 3	0.00
Survival - Year 3 to 4	0.00
Survival - Proportion of Year 4+ that mature to adult	0.00

Biological Variables

Standard Deviation in K

The standard deviation in K (SD in K) represents the year-to-year variability in environmental conditions that influence the population's survival, growth, reproduction and movement. The SD in K is the most influential parameter in our BRT analysis, contributing 49.9% to the model predicting percent decline of the metapopulation at 100 years. Results from the fitted function of

the BRT model and a scatterplot of SD in K versus percent decline (Figure 3-9) indicate that as the value of SD in K increases, the percent decline also increases. SD in K does not appear to be very influential at values less than 0.2. However, the percent decline at 100 years begins to increase with values greater than 0.2. When SD in K is larger than 0.3 the percent decline increases more rapidly, though there is greater variance in the results associated with fewer samples in that range.

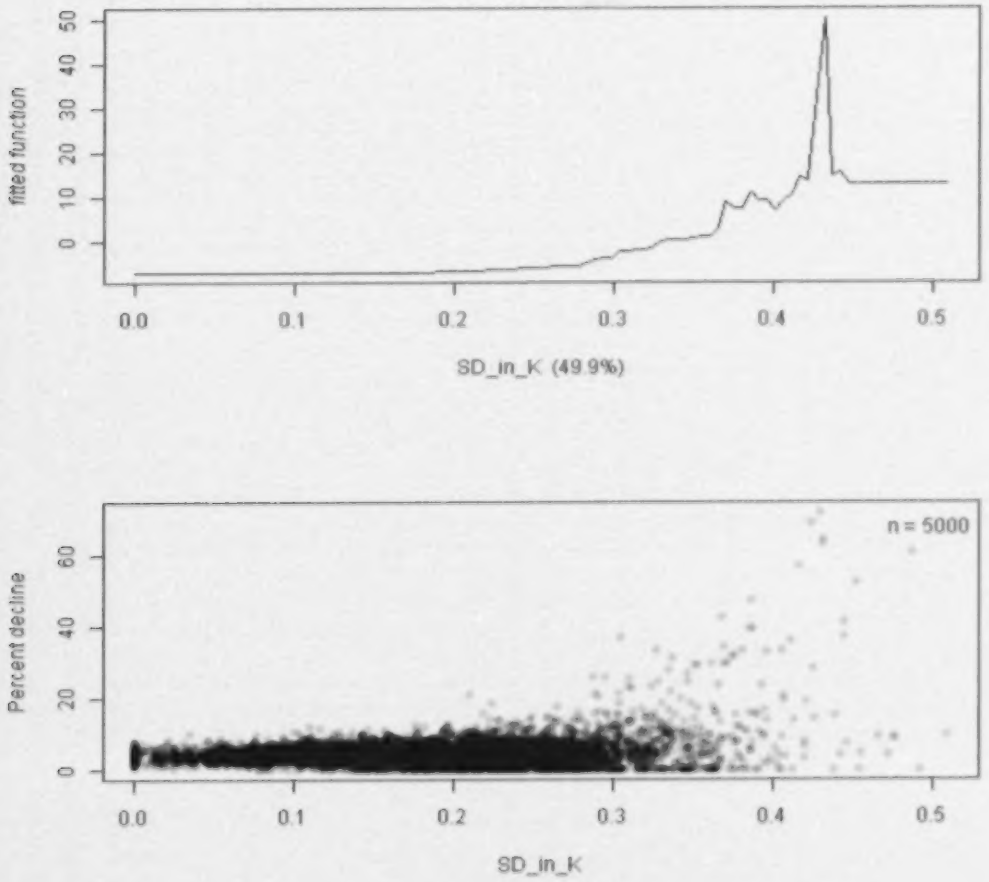

Figure 3-9. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the Standard Deviation in K (SD in K) was normally sampled from a mean of 0.18 with a standard deviation of 0.09.

Initial Abundance of the Metapopulation

Initial abundance represents the total number of adult P. *californicus* in all the populations in the study area at time zero. Initial abundance was the second most influential parameter in the BRT analysis. It contributed 34.4% to the model predicting percent decline of the metapopulation at 100 years. The fitted function and scatter plots of the initial abundance of the metapopulation and the percent decline (Figure 3-10) suggest that when the initial population

size is below 35 million it appears to have little influence, though there is a great deal of variance. Once the population size reaches approximately 45 million there is a slight positive relationship between the initial abundance and percent decline. We interpret this result as an artefact of the way in which commercial harvest rates were implemented in our simulations. In practice, quotas are established on the basis of abundance estimated from fishery-independent surveys. Quotas remain constant and are updated only when new abundance estimates become available. However, areas are rarely revisited to update abundance information. In our simulations, we assume that quotas are never updated with new information, so the same number of individuals are removed during each fishing event for the duration of the time horizon. While the same proportion is removed during the first fishing event (6.6% in a three-year rotation), as populations decline in response to fishing, the number of individuals removed at each fishing event is proportionally larger in populations that were larger at t=0. Therefore populations that are larger at t=0 are likely to exhibit proportionally greater declines in response to harvest. This result underscores the importance of carrying out frequent surveys to update quotas and ensure populations remain above management thresholds.

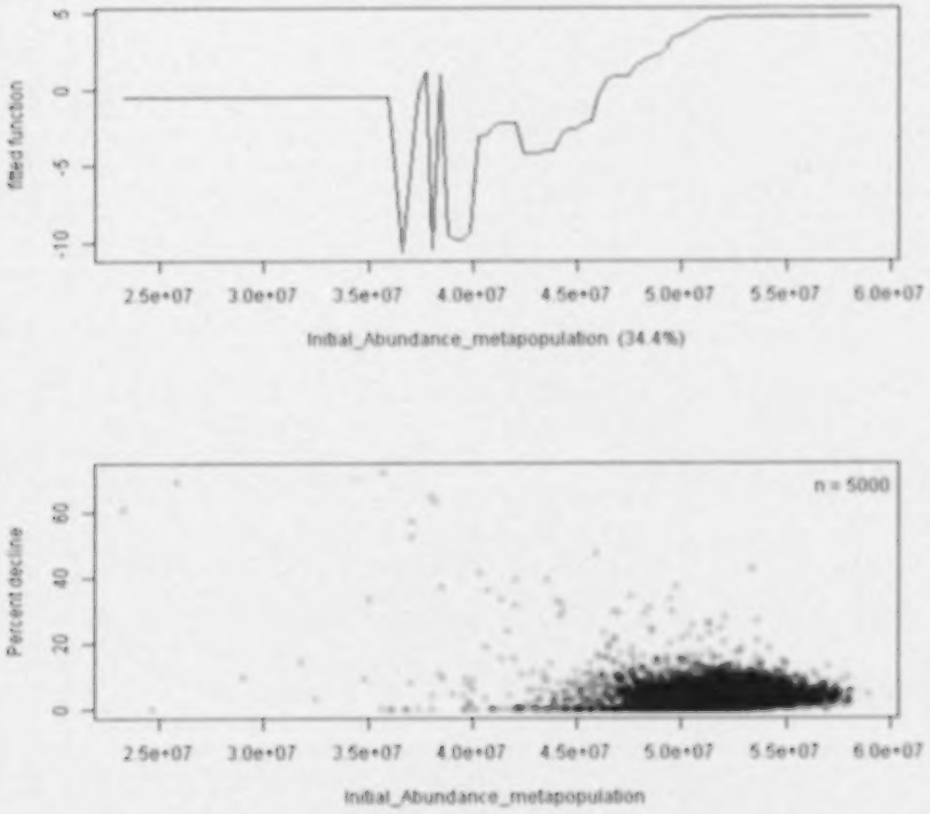

Figure 3-10. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the Initial Abundance of the Metapopulation was the sum of all population abundances varied independently for each population by a CV of 10 %.

Correlation in Vital Rates and Carrying Capacity

Correlation in vital rates and carrying capacity governs the degree to which the dynamics of populations are synchronous. Results from the BRT analysis indicate that in the presented case study the correlation in vital rates and carrying capacity has a very minor influence in the model's predictions of percent decline at 100 years (0.9%). The correlation has almost no influence on percent decline until the correlation reaches about 0.7 (Figure 3-11). At that point there is a slight positive relationship between the amount of correlation between vital rates and carrying capacity and the percent decline.

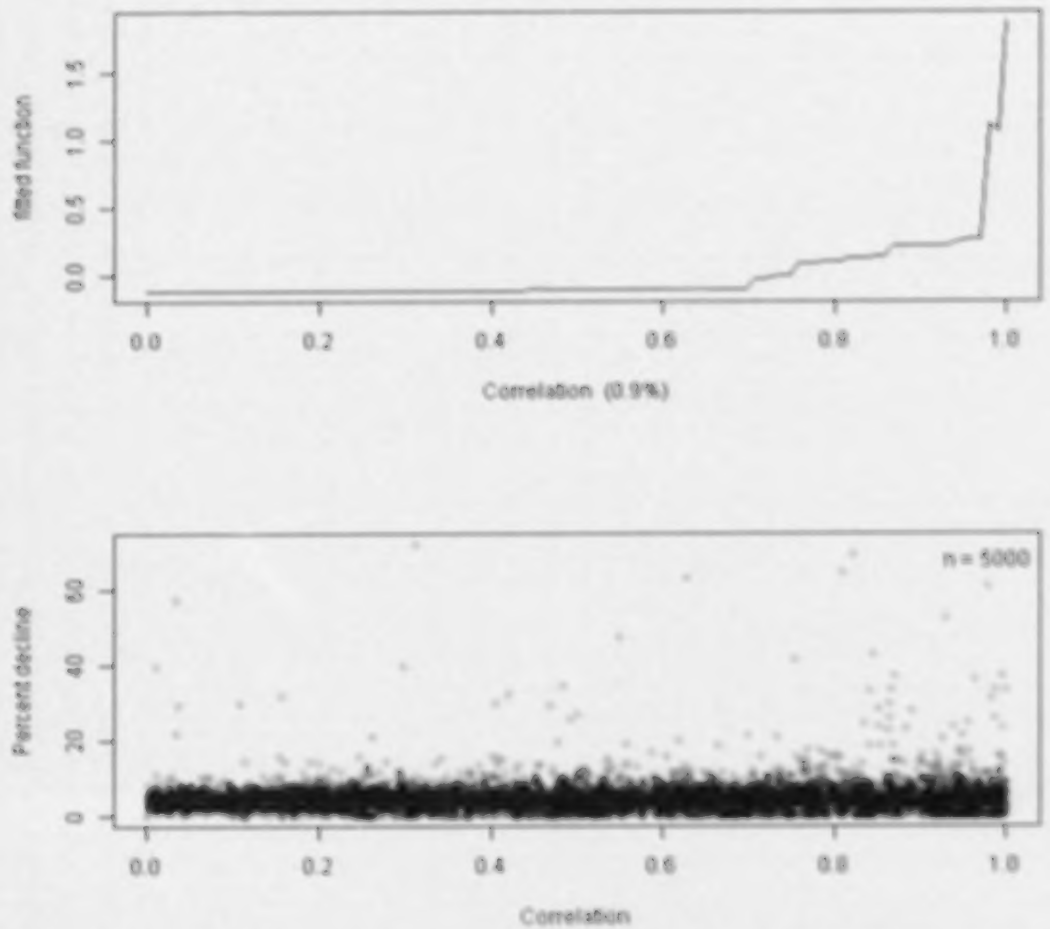

Figure 3-11. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the Correlation in vital rates and carrying capacity was equally sampled from 0.0 to 1.0.

Management Variables

Commercial Exploitation Rates

Commercial exploitation rates were applied at 1- or 3-year rotations to all populations outside of the FCANs. The BRT analysis indicates that commercial exploitation rate is the sixth most important variable when predicting percent decline at 100 years (Table 3-7). Generally, the greater the exploitation rate the greater the declines in the total population (Figure 3-12).

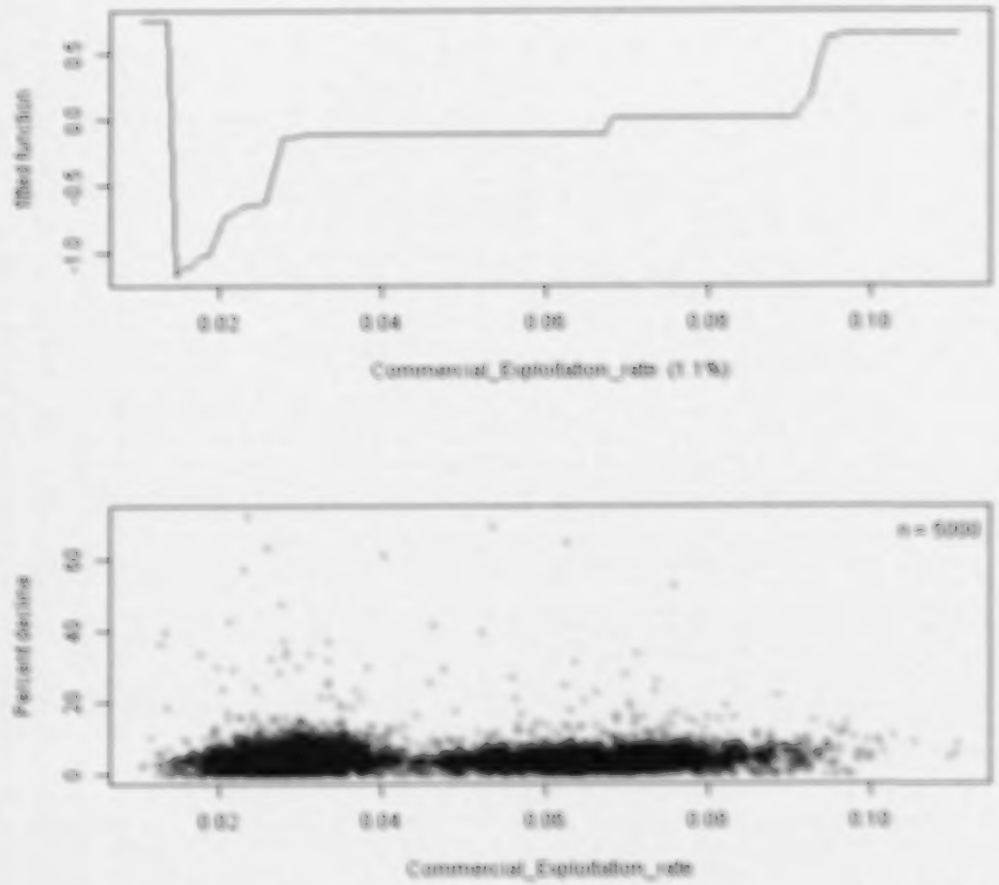

Figure 3-12. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the Commercial Exploitation Rate was sampled from a normal distribution of values with a mean of 2.8 % (annual scenarios) and 6.7 % (3-year rotation scenarios).

Commercial Harvest Frequency

In the sensitivity analysis, commercial harvest frequency is a categorical variable that stipulates whether fishing occurs annually or every 3 years. Annual fishing appears to incur greater declines in the population compared to fishing at a 3-year rotation (5.06% and 4.36%,

respectively). However, in the BRT analysis commercial harvest frequency was not very influential in the model predicting percent decline at 100 years (Table 3-12).

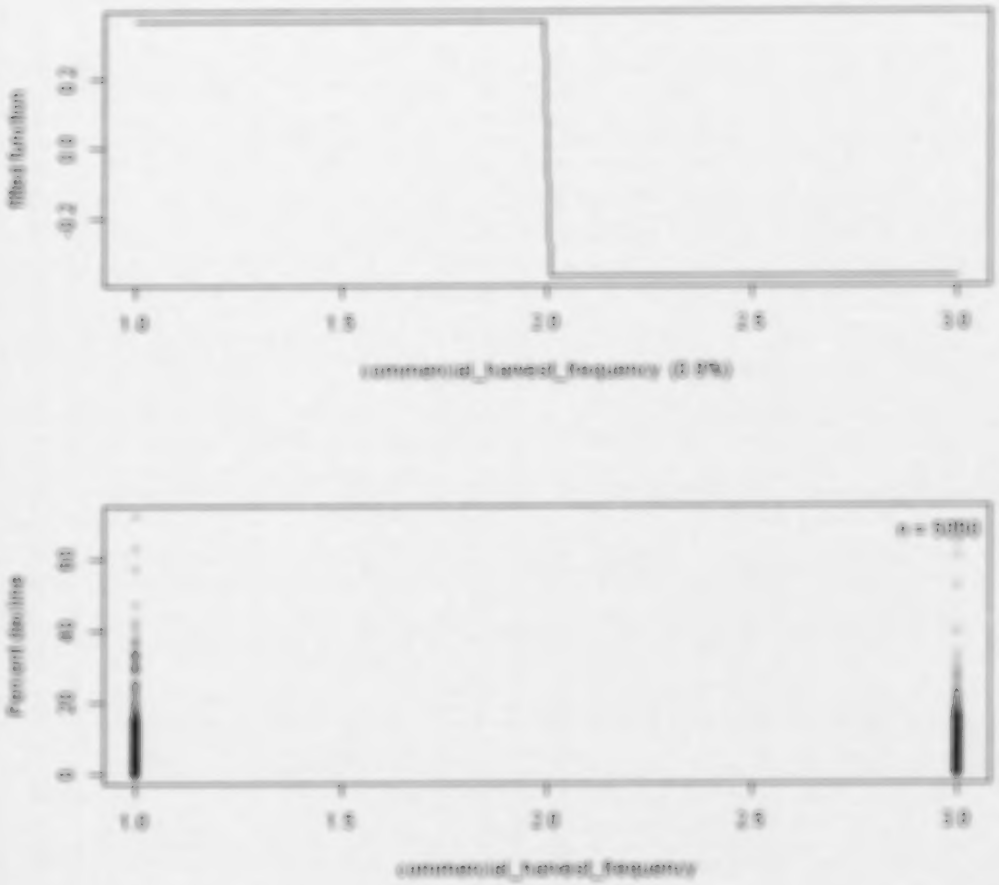

Figure 3-13. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the commercial Harvest Frequency was sampled from annual or 3-year harvesting regime.

Other Exploitation Rates (may include First Nation FSC and Recreational harvests)

Other Exploitation Rates (OER) are removals that occur in populations located within the FCAN designs from either recreational or First Nation harvests. These harvest rates occur annually. BRT analysis indicated that OER was the eleventh most influential variable in the model when predicting percent metapopulation decline at 100 years. A fitted function plot of the BRT model and a scatterplot of OER versus percent decline indicate that as OER increase, population decline also increased slightly at 100 years (Figure 3-14).

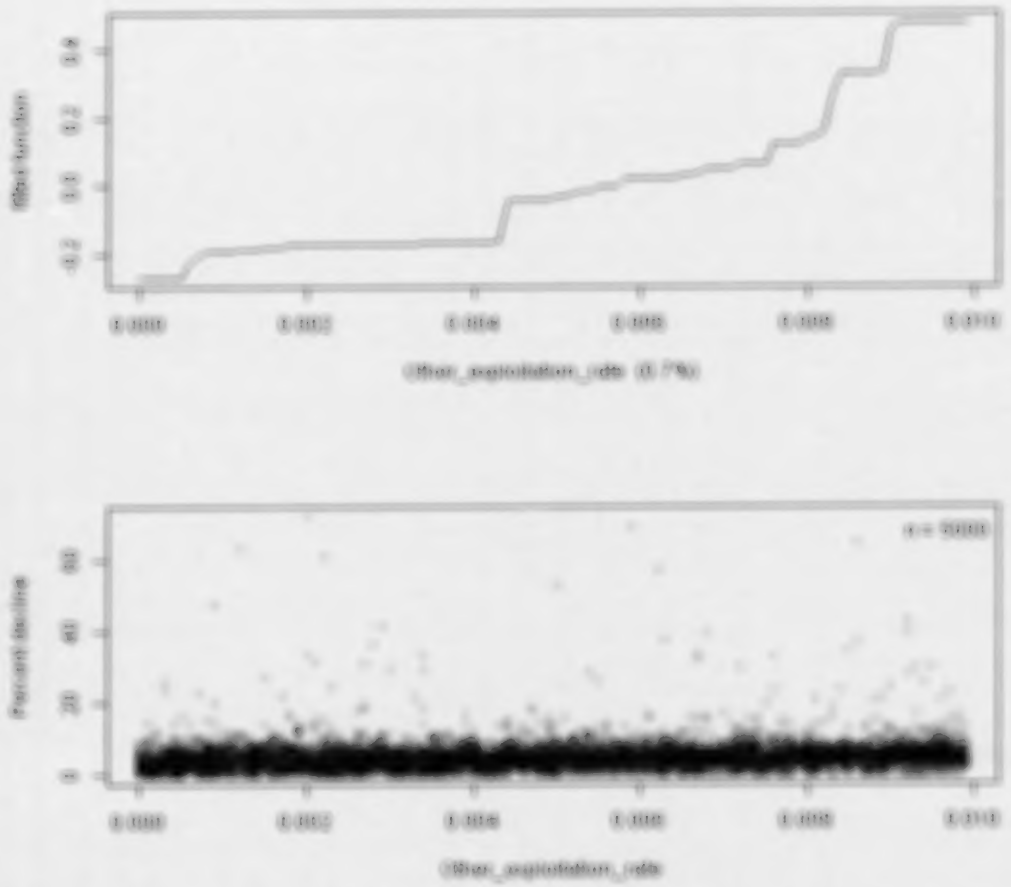

Figure 3-14. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 3,000 sensitivity analysis scenarios where the Other Exploitation Rate was equally sampled from 0.00 to 0.10 %.

Number of PFM Subareas in the FCAN

The number of PFM Subareas in the FCAN is a count of the number of Subareas included in the FCAN. BRT analysis did not identify this variable as having any influence on the model predicting percent decline at 100 years. Declines appear to become more commonly zero when more PFM Subareas are included in the FCAN design (Figure 3-15).

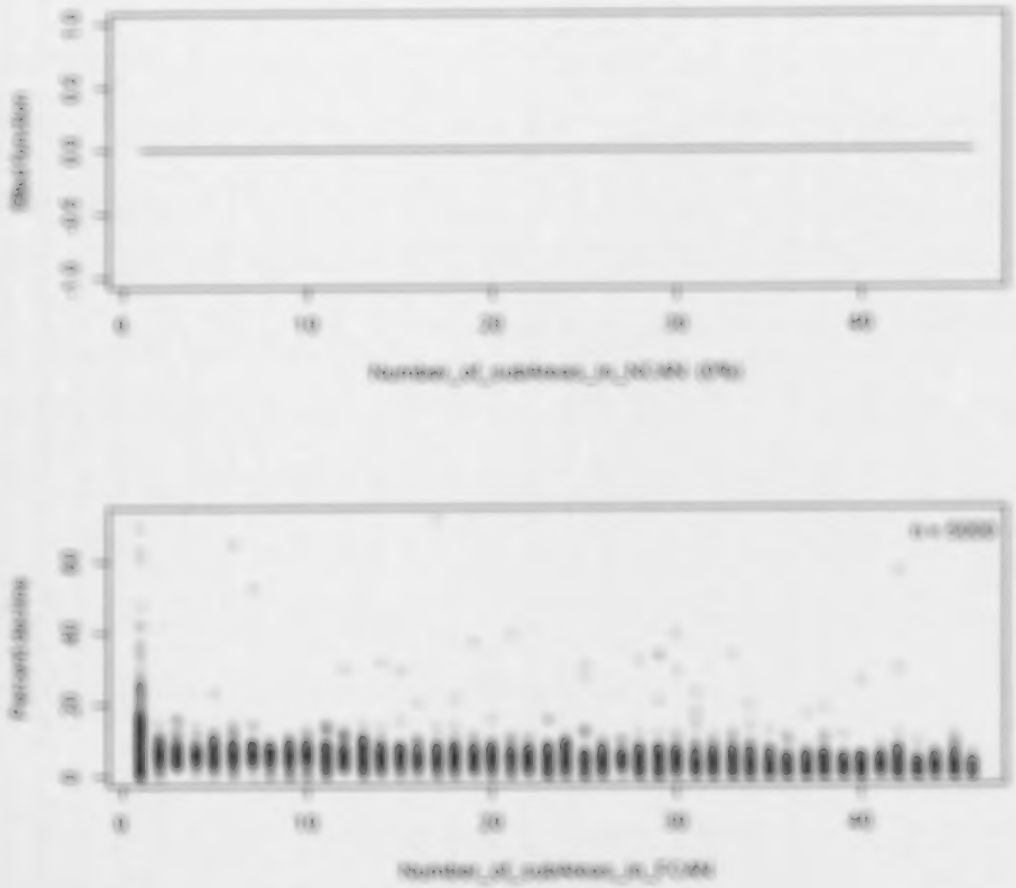

Figure 3-12. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analysis scenarios where the number of Pacific Management Subareas in the Fishery Closure Area Network was equally sampled from 0 to 67.

Number of populations in the FCMA

The number of populations in the FCMA is a count of all the populations selected to be in the FCMA for a particular run. These populations are not subjected to commercial exploitation. The BRT analysis indicates that the number of populations in the FCMA is the tenth most influential variable when predicting the percent decline of the metapopulation at 100 years. The BRT fitted function plot and the scatterplot in Figure 3-19 show that there was a weak negative correlation between the number of populations in the FCMA and percent decline.

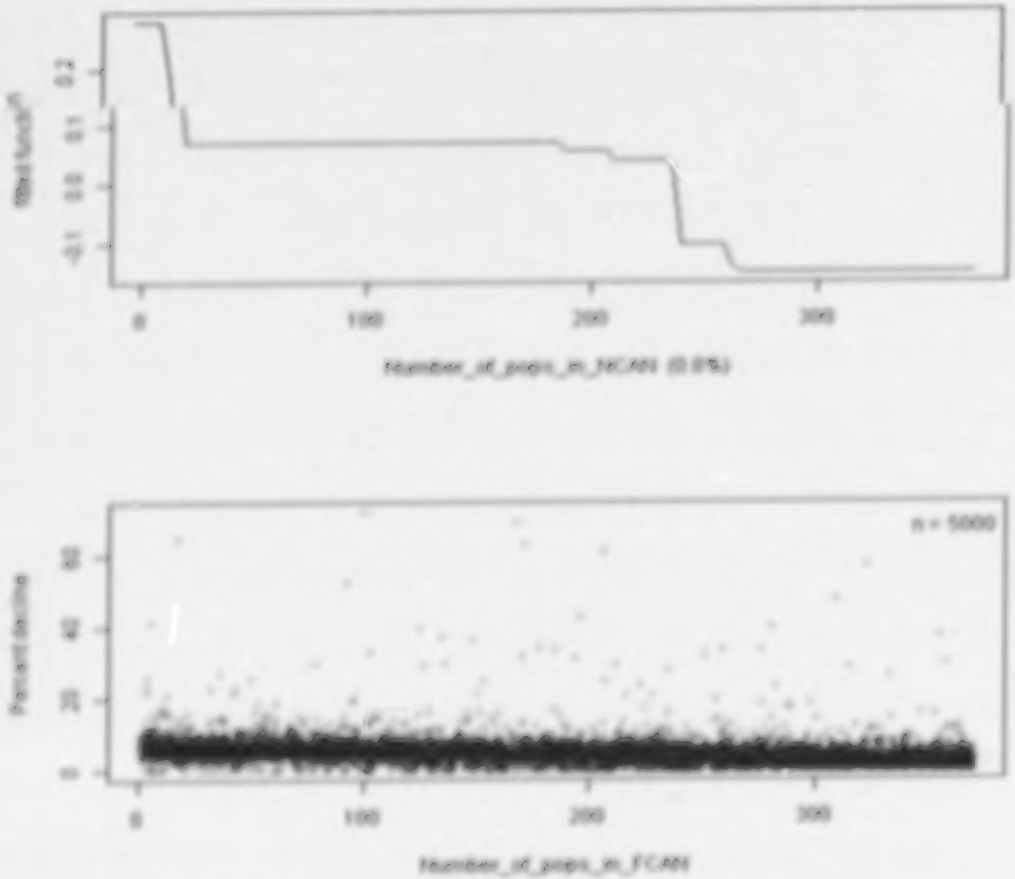

Figure 3-16. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the number of populations in the Fishery Closure Area Network was equally sampled from 0 to 370.

Shoreline Length of an FCAN (of populations only)

Shoreline Length of an FCAN represents the total length of shoreline associated with the populations used in a simulation's FCAN design. In our sensitivity analysis networks that are associated with greater shoreline length have lower declines in population abundance (Figure 3-17).

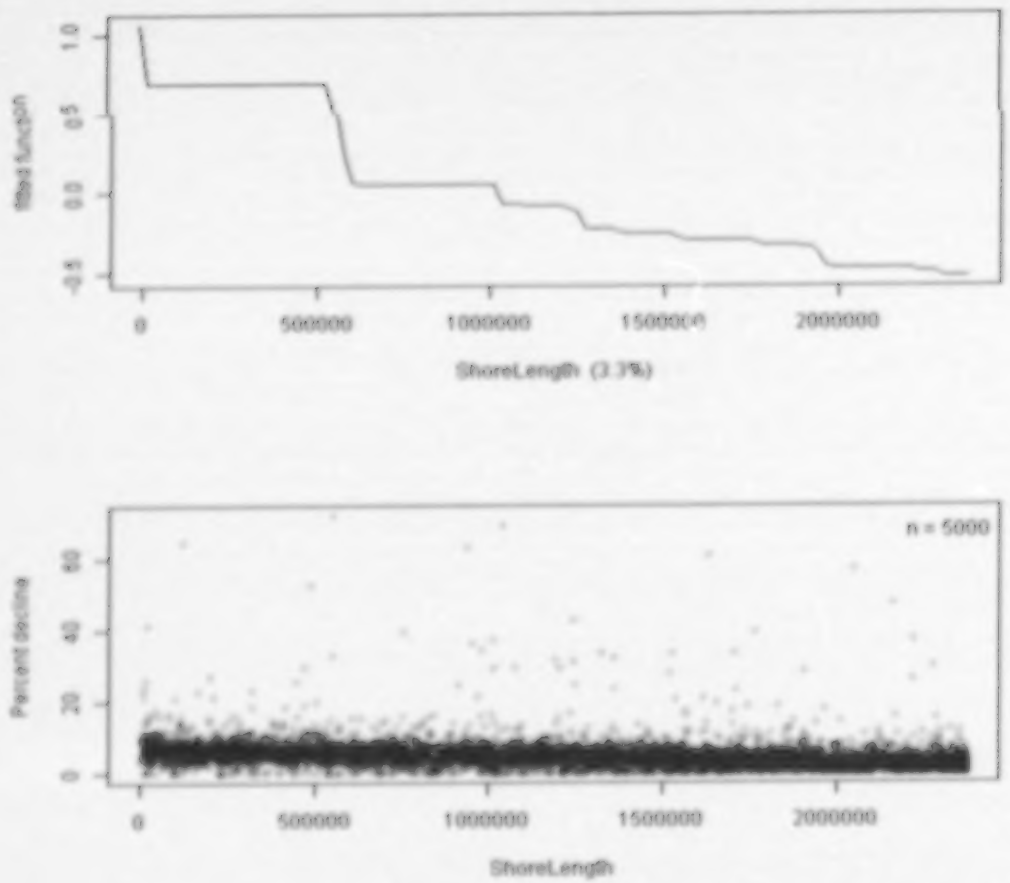

Figure 3-17. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the Shoreline Length is the meters of shoreline affected by the populations contained within the Fishery Closure Area Network for that scenario.

Proportion of Shoreline in the FCAN

The Proportion of shoreline in the FCAN is calculated two different ways depending on whether the FCAN is managed at the population or PFM Subarea scale (see Section 3.2.3.4). Proportion of shoreline in the FCAN is the total shoreline length of all the populations (or PFM Subareas) in the FCAN divided by the entire shoreline length of the study area. The proportion of the total shoreline of PFMA 12 included in the FCAN design has a negative relationship with population decline (Figure 3-18). At proportions of shoreline above 0.40 there only appears to be a small reduction in population declines (Figure 3-18).

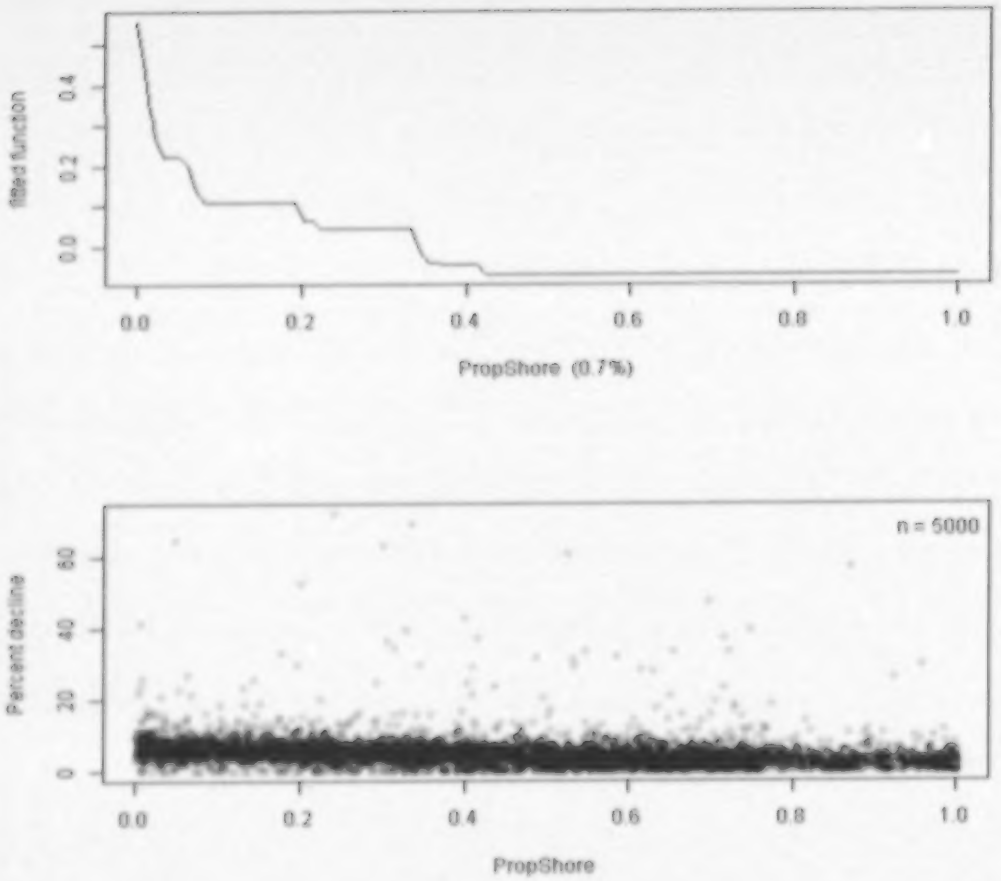

Figure 3-18. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios where the proportion of shoreline affected is the total shoreline length of the populations contained within the Fishery Closure Area Network for each scenario.

Total Area and Area of Suitable habitat in an FCAN

The area within an FCAN is represented by two variables in the analysis: one variable measures the area of suitable habitat (area suitable habitat); and the other measures the area of suitable habitat and the neighbourhood distance buffer (total area). In the BRT analysis the area of suitable habitat and the total area were the fifth and fourth most influential variables, respectively (Table 3-7). For both parameters, as the amount of area in a FCAN increases the percent decline in the metapopulation decreases (Figures 3-19 and 3-20).

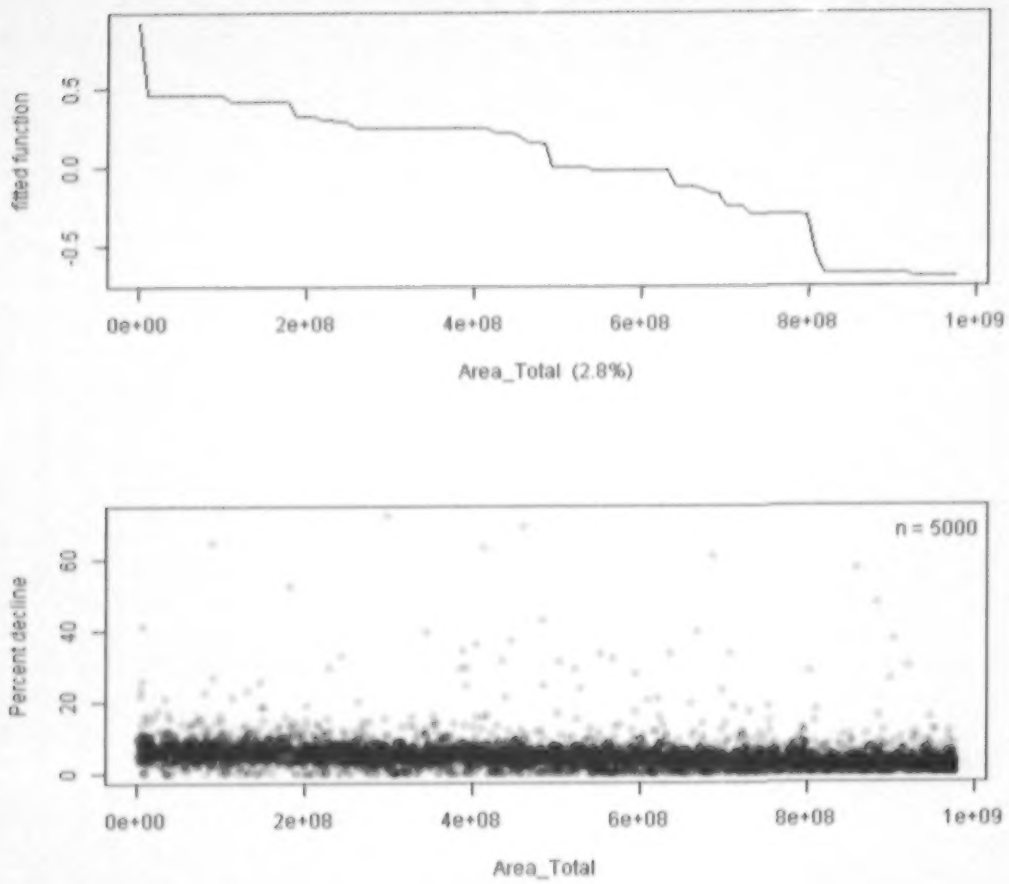

Figure 3-19. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios as a function of the total area (suitable habitat and buffer) of all the populations located in the Fishery Closure Area Network.

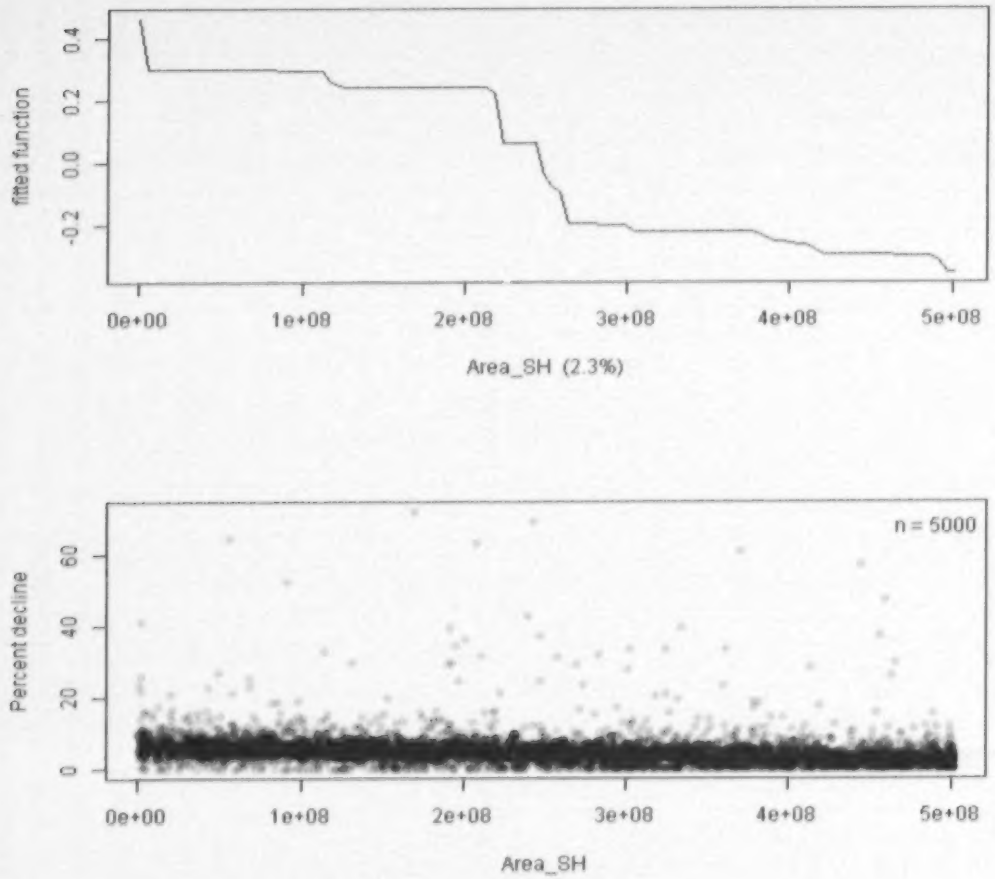

Figure 3-20. The fitted function from boosted regression tree analysis (A) and the percent decline in the metapopulation (B) at year 100, from 5,000 sensitivity analyses scenarios as a function of the area of suitable habitat (suitable habitat only, no buffer) of all the populations located in the Fishery Closure Area Network.

3.5. DISCUSSION

When absorbing, analysing and discussing the output of a large multi-layered sensitivity analysis such as the one presented, it is important to account for the uncertainty associated with many of the input parameters. All the input parameters included here have a certain level of uncertainty and, as the sensitivity analyses indicate, a certain level of influence on the simulation results. While interpreting the simulation results the relative uncertainty and relative influence of each parameter should be taken into account when determining research priorities, management consideration and management action (Figure 3-21).

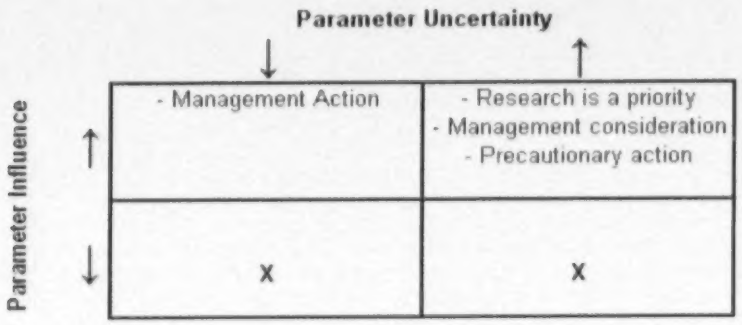

Figure 3-21. The levels of a parameter's uncertainty and influence should be used to inform decisions related to research priorities and management actions. When a parameter's influence is low, management or research action may not be warranted, as learning about or manipulating a parameter will have little influence on the predicted outcomes. However highly influential parameters can exert significant influence on predicted outcomes; advice on actions related to an influential parameter depend on the level of uncertainty associated with the parameter and whether or not the parameter can be manipulated through management action.

3.5.1. Biological parameters

SD in K

Population theory and empirical studies indicate that populations that fluctuate widely from year to year are significantly more vulnerable to declines and extinction than populations that exhibit stable dynamics. Populations can vary in response to changes in environmental conditions, species interactions (including diseases outbreaks, fishing) and changes in a habitat's carrying capacity. In our study the variability in K was approximated on Experimental Fishing Area (EFA) research conducted on *P. californicus* populations between 1997 and 2007 (see analytical methods above). The estimated values for SD in K used here (mean = 0.18, SD = 0.09) is high and may reflect sampling errors associated with survey methods as much or more than actual variations in the carrying capacity of sea cucumber habitat. Thus variability in K is an uncertainty. The estimate of SD in K used in these simulations comes from data that were collected over a small area in each of four EFAs. In any case, our best estimate of the variability in K, and the value used in the baseline scenario, falls below the threshold of where the variability in K has an influence on magnitude of decline (Figure 3-9). As this value is highly influential on simulation results and has a high degree of uncertainty attached to it, conducting research to better estimate the degree to which populations naturally fluctuate from year to year would reduce the uncertainty in simulation predictions and reduce the parameter space that needs to be explored when providing advice on FCAN design. Current best practice when providing advice is to identify designs that are robust to uncertainties, and the degree to which populations vary over time is not only an uncertain parameter, but a highly influential parameter.

Initial abundance

In theory and practice, small populations are generally more vulnerable to declines, extinction and stochastic events. In our case we are simulating large populations that are unlikely to be influenced by demographic stochasticity. In contrast to expectations, there was a positive relationship between Initial Abundance and percent decline at 100 years (as Initial Abundance increased declines increased; Figure 3-10). We interpret this result in the context of current management practices and how these were incorporated into our simulations. In practice, quotas for each PFM Subarea are determined on the basis of an estimate of abundance

calculated using data obtained during fishery-independent SCUBA surveys. The quotas are then fixed at that amount indefinitely or until abundance estimates are updated. Because fishery-independent surveys are infrequently repeated within subareas, or not repeated at all, the fixed quota is applied each year regardless of the true abundance within subareas. (there are a few coastal areas that have been re-surveyed, but most have only been surveyed once). In populations with larger abundances, this fixed harvest amount is larger than in small populations because the quota is set as a percentage of abundance estimates. Because estimates of abundance have a strong influence on the quotas applied within subareas during each harvest year, and because there is a high degree of uncertainty in the initial abundance as well as population trajectories over time, abundances should be estimated in ways that reduce uncertainty and estimated frequently over time so that quotas can be adjusted accordingly. Otherwise, managers run the risk of unknowingly causing undesirable declines.

Correlation in Vital Rates

The correlation in vital rates governs the degree to which carrying capacity and vital rates, like survival rates or fecundity, are correlated among populations.. A high correlation means that in good years all populations have high survival rates, fecundity and carrying capacities, but in bad years all populations do poorly, for instance when regional drivers such as PDO or El Nino negatively affect all populations within a region. Therefore when the correlation is high among populations, the metapopulation is more vulnerable to declines. Consistent with theoretical predictions, as the correlation value in our simulations increased the population declines increased (Figure 3-11). There is a large amount of uncertainty in the real value of correlation in vital rates and carrying capacity in populations in any PFMA in BC, and PFMA 12 is no exception. However, for PFMA 12, using the described assumptions and management regime the correlation in vital rates had a small influence on metapopulation declines and therefore may not warrant extensive research funding at this time. In practice, estimating survival and fecundity rates in multiple populations is very expensive and not typically available for a species.

3.5.2. Management variables

Commercial exploitation rate

The impact of increasing the commercial exploitation rate on the metapopulation was negative at both the annual and 3-year rotational schedules. Commercial harvest catches for sea cucumber in BC are estimated accurately, as harvest landings are all recorded by third party providers and historically there have been few reports or known incidents of poaching in BC. For PFMA 12, using the described assumptions and management regime, commercial exploitation rate over the range explored in our sensitivity analysis had a relatively small influence on metapopulation declines. While this influence is small, managers have complete control over the harvest rate used which may make it an ideal intervention point. We note that higher harvest rates exert a stronger influence on model outcomes based on results not included in this paper. It is also noted that our simulation modelled removals being removed from the PFMA uniformly, while in reality the fishery is patchy with small areas within a PFMA being targeted and harvested heavily. In future runs of the simulation tool it would be more realistic to have scenarios where removals were also patchy within the PFMA.

Commercial harvest frequency

The sensitivity analysis indicated that annual harvest regimes caused higher declines in the population than when a 3-year rotational harvest schedule was implemented, possibly because annual harvesting has a higher exploitation rate (4.2% annually) compared to the 3-year harvest rate (10% once every 3-years). For PFMA 12, using the described assumptions and management regime, commercial harvest frequency had a small influence on metapopulation

decline. However, there is little uncertainty in this parameter as fishery management plans explicitly indicate an annual or 3-year fishing regime. Therefore, harvest frequency, as a management action, can be controlled and may be a useful intervention point.

Other Exploitation Rates

For PFMA 12, using the described assumptions and management regime, the range of other exploitation rates sampled (0% to 1% annually) had a small influence on metapopulation decline at 100 years. However, these values were not determined by data, but are speculations by managers on the true range of other exploitations occurring in the population. Currently there are no landings or reporting methods for *P. californicus* caught recreationally or by First Nations in BC. This parameter is highly uncertain and it is possible that the rate of removal is higher than the ranged used here. Because both recreational catch and First Nation harvesting can be controlled by fisheries managers, more research should be completed to quantify this parameter. This is especially important because simulation results not included in this paper indicate that higher exploitation rates have the potential to be more influential on population declines than those explored in this paper.

Shoreline length

Sea cucumber density is routinely expressed in terms of number of sea cucumbers per meter of shoreline length rather than per unit area when informing fishery management decisions. Our analysis shows that the amount of shoreline associated with a FCAN influences total population declines. Thus, shoreline length could be a useful attribute to consider when designing FCAN.

Total area and area of suitable habitat in an FCAN

While the calculated area is a known value there is a degree of uncertainty as to the true size and location of the habitat patches and density modelling (Section 2). Ideally other mapping layers, with varying levels of uncertainty around patch size and location, would have been included in our sensitivity analyses (see Section 3) in order to quantify the degree of uncertainty and its influence on model outcomes. Overall, area is relatively influential to the simulator and may be a good management intervention point as declines are less severe with increases in either total area or area of suitable habitat (Figure 3-19 and 3-20).

Number of populations in the FCAN

Similar to Area of a FCAN design the results of the relationship between the Number of Populations and metapopulation decline can be used to inform management decisions. Unpublished results indicate that higher exploitation rates increase the negative effect that Number of Populations in the FCAN design has on population declines.

Number of PFM Subarea in the FCAN

Similar to Area of a FCAN design the results of the relationship between the Number of Populations and metapopulation decline can be used to inform management decisions. Unpublished results indicate that higher exploitation rates increases the benefits of increasing the Number of Populations in the FCAN in terms of achieving management goals.

Proportion of shoreline in the FCAN

Similar to the area of FCANs, the results of the relationship between the proportion of Shoreline in the FCAN and decline can be used to inform management decisions.

4. CONCLUSIONS AND OBJECTIVE REVIEW

4.1. ASSESS THE PERFORMANCE OF THE SIMULATION TOOL'S ABILITY TO EVALUATE FISHERY CLOSURE NETWORK DESIGNS FOR SEA CUCUMBERS THAT VARY IN NUMBER, SIZE AND LOCATION, AS WELL AS UNDER VARIOUS SCENARIOS OF DATA AVAILABILITY

Output from comprehensive sensitivity analyses, such as ours, can be used to provide science advice on the amount, number and configuration of habitat patches to include under different management strategies by examining the relationships between metrics and simulation results of interest. For example, Curtis and Naujokaitis-Lewis (2008) used plots of extinction probability as a function of the number of populations and mean geographic distance among populations to estimate the amount and spacing of populations needed to maintain viable metapopulations of sand lizards. In a similar analysis, Curtis and Vincent (2008) calculated the minimum fish size limit needed to meet both conservation and fishery management objectives across a range of exploitation rates. The general approach used in both studies to provide advice can be represented in Figure 4-1.

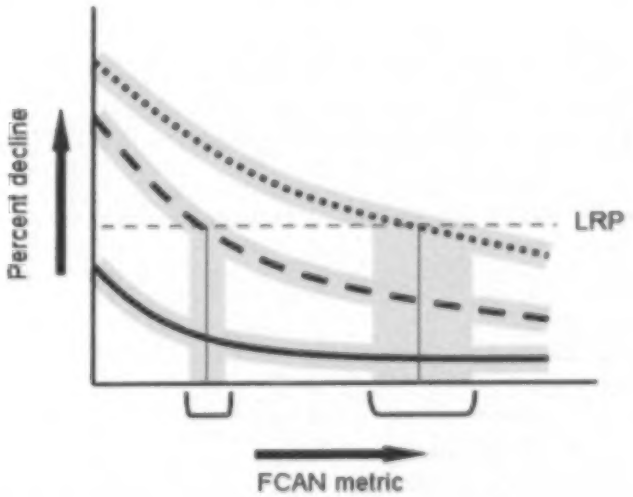

Figure 4-1. A schematic of how varying Fishery Closure Area Network (FCAN) metric (such as number of PFM Subareas included in FCAN) can be used to predict percent decline in the population and in achieving FCAN objectives (in this case remaining below the limit reference point; LRP). The three different lines (solid line, hashed line and dotted line) represent different parameter values (for example low, medium and high other exploitation rate).

In the schematic, percent decline is plotted as a function of an unspecified FCAN metric and three hypothetical relationships between the two variables are plotted. In all cases, there is an influence of the FCAN metric (e.g. number of populations in FCAN or total area of FCAN) on percent decline, but the form of the relationships differ. The dotted and dashed lines represent two cases in which the relationship between percent decline and the FCAN metric intersect a specified management objective, in our case for *Parastichopus californicus* the LRP. We could use those relationships to provide science advice on the attributes of the FCAN required in order to prevent populations from falling below the LRP, along with confidence intervals. Those attributes might be the number of populations, or total habitat area, or shoreline length needed

in the FCAN design to prevent populations from falling below the LRP. By contrast, the solid line represents a situation in which populations never fall below the LRP regardless of the FCAN attribute. This situation represents the analysis in our paper: given the specified management scenario, input parameters and ranges explored in our sensitivity analyses, our simulations suggest that at the scales of PFMA 12 and its subareas, sea cucumber populations are unlikely to fall below the LRP regardless of how many populations or PFM Subareas are included in the FCAN. Very few scenarios in our comprehensive sensitivity analysis led to PFM Subareas falling below the LRP over 20 or 100 years. When we plot percent decline as a function of FCAN metrics in our study, the relationships consistently fall below the specified limit reference point (i.e. 50% of B_0). We interpret these results as meaning that the current management strategy of 3 year rotations coupled with a precautionary harvest rate is likely to be sustainable over the short and long term. This interpretation is consistent with previous stock assessments using quite different analytical approaches for *P. californicus* and which were used as the basis for setting the precautionary harvest levels simulated in our analyses (Hand et al. 2009).

An important concept to bear in mind is that the required number, size and configuration of habitat needed to meet conservation or fishery management objectives depend not only the strength and form of the relationships between these metrics and the likelihood of achieving the objectives, but they also depend strongly on interactions among variables and on the objectives themselves. For example, in their analysis of minimum size limits, Curtis and Vincent (2008) noted a strong interaction between the size limit needed to meet multiple objectives and the harvest rate; more stringent size limits were needed to meet conservation and fishery management objectives when harvest rates were greater. They also noted that as the stringency of the conservation or fishery management objectives increase so too did the stringency of the management strategy. In our case, if the LRP were set at 5 or 10%, our relationships would likely intersect the LRP and allow us to provide quantitative advice on the FCAN attributes required to achieve objectives. Based on simulation results not included in our paper, increases in commercial and other harvest rates would change the form of the relationship between percent decline and FCAN attributes such that they could intersect the LRP. As we were not asked to consider a broader range of harvest rates in our analyses, these results are not included. But we emphasize the importance of considering interactions among variables and impact the nature of the conservation or fishery management objectives could have on the science advice that could be provided. We also note that if we applied this set of tools to other populations, or other species, the general conclusions could be very different.

4.2. ASSESS THE PERFORMANCE OF THE SIMULATION TOOL'S ABILITY TO EVALUATE ALTERNATIVE FISHERY CLOSURE NETWORK DESIGNS FOR SEA CUCUMBERS BASED ON A RANGE OF PERFORMANCE MEASURES AND PLAUSIBLE COMMERCIAL AND FIRST NATIONS FISHERY MANAGEMENT SCENARIOS.

The performance measures used to evaluate alternative fishery closure network designs in this paper were the percent decline, the number of Subareas that fell below LRP, and the proportion of years that any Subarea fell below LRP at set intervals (20 and 100 years in this case). The code is already designed to record population occupancy and probability of extinction, as well as cumulative harvest over time. In addition to these metrics, the code we used to build our simulator is flexible enough to allow users to evaluate alternative FCAN designs based on any performance measure that can be calculated from the predicted/simulated distribution and abundance patterns over space and/or time. There is the potential to build in other types of indicators, but these would need to be assessed in terms of their ability to be included in the simulator.

The code allows users to simulate a variety of plausible commercial and other fishery management scenarios. It can incorporate up to two types of harvest (e.g., commercial and other harvest rates), and those harvest rates can be applied to any stage at any frequency and across any spatial scale that is equal to or larger than the population scale (e.g., populations, Subareas, PFMAs). Harvest can be applied as a proportion of the population or at a fixed number of individuals throughout time.

4.3. EVALUATE UNCERTAINTY IN PARAMETER ASSUMPTIONS AND SIMULATION TOOL RESULTS AND, BASED ON SENSITIVITY ANALYSIS, PROVIDE RECOMMENDATIONS FOR WAYS TO REDUCE UNCERTAINTY.

Several parameters used in the presented tools were unknown for *P. californicus* and therefore are uncertain. The sensitivity analyses presented in the paper is a tool to quantify the relative influence of variables on model results. We have described the degree of uncertainty in the variables that were identified as being highly influential in the current analysis. One important source of uncertainty that was not considered is role of interactions between variables in model outcomes. Due to time constraints, there was insufficient time to test the variables used in the sensitivity analyses for interactions. This step is especially important, as interactions between variables can be strong and could change the relative influence they have on simulation results. If the presented suite of tools is used in a full analysis, interactions between variables should be fully explored. This would reduce the uncertainty in parameter influence and make a synthesis of parameter influence more defensible.

Research priorities can be developed from the outputs of these tools by comparing the relative influence parameters have on management indicators (areas of suitable habitat, population density and size, percent population decline, remaining above the LRP, etc) and ascertaining the certainty of the parameter. Reducing the uncertainty in some of the parameters may be possible through research (e.g., standard deviation in K) while research into other parameters may be cost/time prohibitive (e.g., survival of each year class of juveniles in the wild).

4.4. ASSESS THE APPLICABILITY OF THE SIMULATION TOOL TO OTHER LOW-MOBILITY, SHALLOW-WATER BENTHIC INVERTEBRATES.

This suite of tools can be used for a variety of low-mobility shallow-water benthic invertebrate species in BC (e.g. Geoduck (*Panopea generosa*) and Red Sea Urchin (*Strongylocentrotus franciscanus*)). Indeed, a similar analysis is being used to evaluate the influence of poaching on the dynamics of abalone populations in Barkley Sound (Camacho et al. in prep). The predicted habitat suitability models and predicted density models could be constructed for many species of low-mobility benthic invertebrate species as long as biologically relevant environmental and population data exists for the area of interest. The environmental data used here were highly detailed due to the extensive research that has focused on the Broughton Archipelago. Sensitivity analysis in the habitat suitability and density models explored different resolutions of environmental data and found that there was no significant difference in the performance of the model for PFMA 12. Similar models can be built at a variety of resolutions for any coastal area where environmental data exist.

The metapopulation dynamics model could easily be re-tuned for a different species by programming the life history parameters specific to the target species. In fact, some species may have less uncertainty in some of the parameters used in the model, which could reduce uncertainty in the results. The dispersal model is a basic model that again could be fine-tuned for another species, incorporating any known information on larval pelagic duration, behaviour and movements.

Finally, the fisheries management model can be re-written to incorporate the management regime used for the target species. All in all these tools could be fully replicated and customized for another species, either in part or in full, but only if there was the expertise available to complete these tasks. It is important to note that while these are valuable tools, they cannot be re-tuned to other species nor re-run for *P. californicus* unless the users have expertise in spatial analysis, simulation modelling, the R programming language, and RAMAS software.

4.5. PROVIDE A DISCUSSION ON THE SUITABILITY OF PROXIES OR ALTERNATIVE METHODS TO IDENTIFY CANDIDATE COMMERCIAL FISHERY CLOSURE LOCATIONS FOR LOW-MOBILITY BENTHIC INVERTEBRATES.

The suitability of proxies or alternative methods for identifying candidate FCAMs depend first and foremost on the management objectives. For example, if the management objective is simply expressed as a desired proportion of suitable habitat (e.g., 50% of available habitat), a map-based approach would be sufficient. Map-based approaches could range in complexity from simply plotting known habitat to modelled predictions of suitable habitat, as described in Section 2. Tools such as MARXAN could be used to optimize the placement of closed areas when there are also other objectives, such as minimizing cost. The benefit of using these approaches is they are relatively straight-forward to apply, so long as you have the appropriate data. The disadvantage is that they typically only provide a snapshot of what is in fact a very dynamic system.

When objectives are expressed in terms of the change of distribution or abundance of a species over time, more sophisticated tools are required. These tools must have the capability to account for dynamic processes over time, as well as methods to account for uncertainty. The strength of the set of tools that we present is that they can be applied in either scenario. The component parts can be used individually, or as a combined tool. The main drawback of our simulation approach is the level of expertise and time required to carry out the analysis.

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